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SCLEROTINIA BIFRONS

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(WITH 2 FIGURES)

The report of the perfect stage of *Sclerotium bifrons* from material collected in Colorado in 1929, while on a collecting trip with Dr. Paul F. Shope of the University of Colorado,[1] has caused considerable discussion and given rise to much misunderstanding. The following notes were prepared in 1940 in reply to an article by our late friend and colleague H. H. Whetzel.[2] It is regretted that they could not have been published during his lifetime, but since all points have been freely and sometimes "heatedly" discussed with him, the writer has no misgivings in presenting them now, hoping that they may correct some of the misinformation given out regarding our Colorado fungus. The fungus in question was collected near the University of Colorado summer camp after a special search for the perfect stage of the poplar sclerotium.

In a ravine[3] not far from the camp, in as pure a stand of *Populus tremuloides* as could be found, and where the trees were at the time loaded with the sclerotia of *Sclerotium bifrons,* we finally succeeded in locating sclerotia on the ground producing a perfect stage in great abundance. Hundreds of sclerotia, each with a

[1] MYCOLOGIA **22**: 3, 1930.

[2] MYCOLOGIA **32**: 124–127, 1940.

[3] A ravine was selected since the conditions of moisture seemed more favorable for the growth of the fungus if it did occur.

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clump of stalked fruiting bodies, were collected. The ascomycete was active and the minute apothecia puffing spores like miniature steam engines, although it was late in the month of July. In our account of the trip this was reported as the perfect stage of *Sclerotium bifrons* under the name of *Sclerotinia bifrons*. It was later observed under other stands of poplars in that general region.

In the meantime we learned that Professor Whetzel had been collecting the perfect stage of *Sclerotium bifrons* in the East and, knowing that he was working on the group, Colorado material was transmitted to him for study. Comparison by Whetzel soon revealed the fact that we had not one but two species on what had been regarded as *Sclerotium bifrons*. Immediately Whetzel assumed that his was the orthodox perfect stage of *Sclerotium bifrons*, and the fungus reported by us as such was an "imposter."

In an attempt to discredit our observations, two lines of argument were adopted by him. First he claimed that our fungus was not a *Sclerotinia*, but a *Helotium* growing on *Sclerotium bifrons*. This could have been possible, but was scarcely likely. Later he abandoned this line and conceded that what we had from Colorado was a *Sclerotinia*, but that it did not come from the poplar *Sclerotium bifrons*. Just what it did come from he did not know. All this argument was purely academic since he had never collected in Colorado.

I might illustrate Whetzel's course of reasoning in the following manner: If one should go out into an apple orchard and find a crabapple tree loaded with a certain kind of crabapples, and at the same time find numerous "free lying" apples of the same kind under the tree, he would naturally assume that the apples on the ground came from the branches overhead. If his friend, who had not visited this orchard, should argue that the apples on the ground did not come from the tree under which they were found, but from some other tree, although no other tree was known to produce this kind of apple, and from such other place, he did not know where, and that they were transported to this particular apple tree by some unknown agent, he did not know what, the argument would be too "far fetched" and ridiculous to even merit serious consideration. Yet this is exactly the line advanced by Whetzel in his determined effort to discredit the field observations of Dr. Shope and myself,

since these observations seemed to conflict with his own made in the East.

If Whetzel had worked as hard to explain our observations made in Colorado, as he did in his futile attempt to disprove them, without any first-hand field observations, he would have had no difficulty in concluding that there was no incompatibility between these two claims, but that in reality we have two species of *Sclerotinia,* both occurring on what was supposed to be the same sclerotium on the same host. This might be accounted for in the following manner:

Populus tremuloides as it occurs in the Rocky Mountain region is regarded by botanists here as a distinct variety from that occurring in the East. Therefore, *Sclerotium bifrons* of the Rocky Mountain variety of *Populus tremuloides,* while to all outward appearances identical with the eastern form, and so regarded by Ellis himself, is in reality different, these differences so far as observed to date manifesting themselves only in the perfect stage. On this assumption, our apothecial stage collected in Colorado is the perfect stage of the Rocky Mountain form of *Sclerotium bifrons,* while those collected in this region (New York) are the perfect stage of the Eastern form of the same species. From this we would conclude that what has been regarded as *Sclerotium bifrons* by various mycologists, including Ellis himself, really represents not one but two, and possibly several distinct species. A similar situation has been reported by Drayton [4] and others, where three distinct species of *Sclerotinia* have been connected with what has commonly passed as *Botrytis cinerea* as their conidial stage. Whether the species on poplar can be distinguished in the sclerotial stage remains to be seen, but it is quite evident, as Whetzel has pointed out, that in their perfect stages they are two very different species.

Another bit of evidence advanced by Whetzel to prove that our Western species is not *Sclerotinia bifrons,* is the fact that according to his records *Sclerotinia bifrons,* as he knows it in the East, discharges its spores over a period of ten days to two weeks during the time when the leaf buds are bursting and the young leaves unfolding, which would be about April or May, while the plants of

[4] MYCOLOGIA 31: 485–489, 1939.

our species reported from Colorado were found shooting their spores vigorously late in July. Here again Whetzel is comparing the behavior of two different species. It must be borne in mind that even the same species of fungi do not behave in the same manner at an elevation of 9,600 feet that they do a few hundred feet above sea level. The writer has often observed high in the Rocky Mountains in August species of fungi which would be known in this locality (New York) only in early spring. Consequently, we would expect that a high altitude species of *Sclerotinia* would not mature and discharge its spores at the same season of the year that a low altitude form of the same genus might do.

The writer has not had a chance to study the Colorado species in the field over a long period of years, as Whetzel has the Eastern form, and is therefore unable to furnish all the details as to time and manner of host infection and length of fruiting period, as could be done if we lived in the region where this species occurs. Doubtless this will be done at some time, by some local student, and the story will be made complete.

Still another point frequently raised by Whetzel, and emphasized in his paper, is the fact that our species in Colorado occurs "On the ground from *free lying* sclerotia entangled in leaf debris, under trees of *Populus tremuloides*," and that the sclerotia were never found producing apothecia while attached to the leaf on which they were said to be produced. This may be explained by the fact that the sclerotia when mature drop out of the leaf and fall to the ground unattached, although many do also fall with the leaves. Whether those that fall with the leaves are sufficiently mature to produce apothecia is not known, but if they do the leaf tissues are pretty thoroughly disintegrated. In order to show the way in which the sclerotia do dehisce from the leaves, the writer is offering in evidence a photograph (FIG. 2) of the leaves taken in the Rocky Mountains, which are apparently full of shot holes where the sclerotia have been released. This will account for the production of apothecia on "free lying" sclerotia. Whether the apothecia are produced the following season after the sclerotia are released, or later, we have no means of knowing.

The reader is asked to note carefully the variation in the form of the shot holes after the dehiscence of the sclerotia, especially

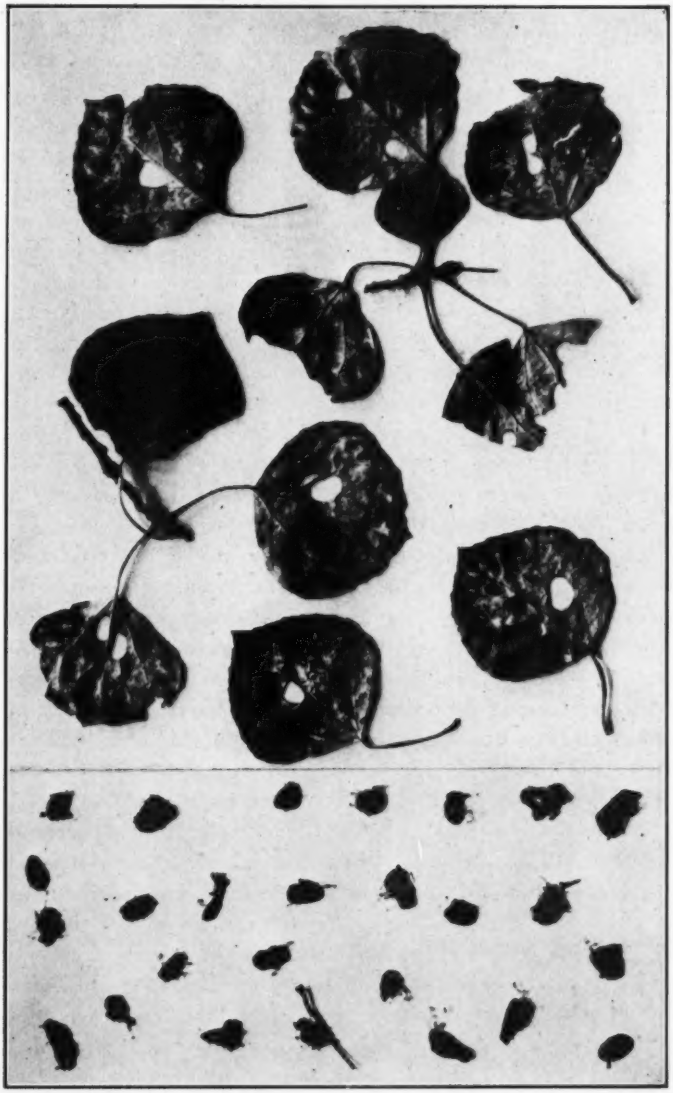

FIG. 2. *Sclerotinia bifrons.*

the tendency to assume a semi-triangular form with rounded corners. The reader is then again asked to compare these with the free-lying, apothecia-producing sclerotia, bearing in mind that these are photographs and not drawings (FIG. 2). So far as size is concerned, there is no discrepancy between size of the holes and sclerotia which are reported to have come from them. The resemblance in size and form of those on the ground and those on the tree is alone evidence that the apothecia-producing sclerotia did come from the poplar leaves, if we needed any further evidence. The origin of the sclerotia was so obvious to us working in the field in Colorado that no such extraneous evidence is necessary, but is cited here for the benefit of those who have not had the privilege of seeing the fungus in the field, and who might be misled by arguments advanced to disprove our observations.

Perhaps the most striking piece of evidence advanced by Whetzel is his announced discovery in the debris accompanying specimens of our fungus sent him from Colorado of foliar remnants of some other plant than the poplar. He immediately assumes that this unknown plant "may represent the real suscept" of our *Sclerotinia*. He does not know what the plant is since no other in the Rocky Mountains is known to produce this particular type of sclerotium. Neither does he explain how these fruiting sclerotia came to be accumulated in such large numbers under poplar trees which were seen to be producing the same type of sclerotia at the same time, nor why they were not found in any other situation during our summer's work in the West. Such minor details are lightly brushed aside.

Having thus thoroughly convinced himself that the poplar *Sclerotinia* reported by us is not of poplar origin at all, and knowing that his *Sclerotinia* in the East is, he feels perfectly justified in taking over the name applied to our fungus ten years earlier and applying it to his own, and recording our fungus as a new species of his own under the name *Sclerotinia confundens* Whetzel. Misdetermination of host is no valid ground for changing the name of a fungus, even if proven. In this case not one shred of real evidence has been advanced to disprove our claim or to substantiate his own. To attempt to change a name on mere suspicion of error is not only illegal but inexcusable.

SUMMARY

The specific name *confundens* is untenable since the fungus described as "*Sclerotinia confundens* Whetzel sp. nov." in 1940 had been previously recorded under the name *Sclerotinia bifrons* Seaver & Shope in 1930, and reported as the ascigerous stage of *Sclerotium bifrons* from poplar trees in Colorado. Whetzel's claim (MYCOLOGIA **32**: 125) that the Seaver and Shope report was based on an "error in identification," apparently referring to the fungous host, was absolutely groundless and unjustified, but, even if true, would furnish no valid reason for the rejection of the Seaver and Shope binomial and the redescription of their plant as a new species ten years later under a different name, and finally applying the rejected binomial to another plant thus establishing a homonym which could have no legal standing and which under the International Rules **must** be rejected. Obviously *Sclerotium bifrons* on poplars like the so-called *Botrytis cinerea* has more than one ascigerous stage. The synonymy of the two species on poplar sclerotia would then be as follows:

1. SCLEROTINIA BIFRONS Seaver & Shope, 1930 (Not *Sclerotinia bifrons* Whetzel, 1940), Syn. *Sclerotinia confundens* Whetzel, 1940.
2. SCLEROTINIA WHETZELII Seaver 1940, Syn. *Sclerotinia bifrons* Whetzel, 1940 (Not *Sclerotinia bifrons* Seaver & Shope, 1930).

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EXPLANATION OF FIGURES

FIG. 1 (frontispiece). *Sclerotinia bifrons.* A branch of *Populus tremuloides* showing healthy and infected leaves. Below, photograph of three sclerotia somewhat reduced. Below, enlarged photograph of two sclerotia with apothecia. Enlarged photographs were made by Dr. Paul F. Shope from fresh material collected in Colorado. The photographs were hand colored by Fleda Griffith.

FIG. 2. *Sclerotinia bifrons.* Above, photograph of poplar showing shotholes where the sclerotia had dropped out. Below, photograph of a number of sclerotia producing apothecia. These photographs were made from dried material.

A SYNOPSIS OF THE GENERA AND SPECIES OF THE SCLEROTINIACEAE, A FAMILY OF STROMATIC INOPERCULATE DISCOMYCETES

H. H. Whetzel [1]

(with 36 figures)

At the urgent behest of my long-time friend, the well-known mycologist, Dr. H. S. Jackson, I have been persuaded to present a synoptical view of the group of stromatic inoperculate Discomycetes with which I have busied myself at odd times during the past forty years. It is with considerable misgiving that I do so. A work of this sort had far better been left until I had completed monographs of the individual genera which comprise the family here under consideration. In spite of the fact that I have been free of teaching responsibility for the past few years, my progress with these monographs has been slow indeed. The only alibi I can offer is that I have had poor health since 1939 and have experienced the slow down which aging seems to impose. Of the fifteen genera which are here characterized I have thus far monographed but four, *Septotinia* Whetzel (**1937**), *Martinia* Whetzel (**1942**), *Lambertella* v. Höhnel (Whetzel **1943**), and *Coprotinia* Whetzel (**1944**). I have also completed a partial monograph of *Sclerotinia,* ten species of which are fully treated in "The cypericolous and juncicolous species of *Sclerotinia,*" soon to appear in Farlowia. One of my former students, Dr. W. Lawrence White (**1941**), has monographed the genus *Rutstroemia,* another, Dr. Freeman Weiss, established the monotypic genus *Ovulinia* Weiss (**1940**), while a third, Dr. E. E. Honey, has in final stages of preparation a monograph of the genus *Monilinia.*

[1] Professor Whetzel died Nov. 30, 1944. This posthumous paper, unfinished at his death, was completed and submitted for publication by H. M. Fitzpatrick. See footnote 6. Financed in part by funds donated by the Mycological Society of America.

While my work on several of the other genera is well along, the rate at which these monographs have been appearing suggests that I may not live long enough to complete them all, even with the able coöperation of my students. For these reasons I commit myself to the following diagnoses of the family and genera and to assignment of species in as far as my present knowledge of these forms appears to warrant. I reserve the right, however, to repudiate any and all statements or conclusions which may later be found fallacious. I have no doubt that there are errors of omission as well as commission. It has not been possible to investigate every genus, let alone every species, with the thoroughness that such an undertaking as this requires. While I have personally studied in the living condition most of the forms here treated, I have had to rely wholly or in part on the work of others for some of them.

I am deeply indebted to so many former students and colleagues all over the world that I cannot undertake to name them. To each one who with specimens or other material contributed through the years to my studies on the stromatic inoperculate Discomycetes I here express my warmest thanks and cordial appreciation. A special grant by the Cornell trustee-faculty committee on research has greatly facilitated the preparation of this paper, and for this I am most grateful.

GROUNDS FOR ESTABLISHMENT OF THE FAMILY SCLEROTINIACEAE

The most recent attempt to provide a more satisfactory classification of the inoperculate Discomycetes is that of Nannfeldt (**1932**) in his "Studien über die Morphologie und Systematik der nichtlichenisierten inoperculaten Discomyceten." He undertakes a reorganization of the earlier systems of classification based on a study of the anatomical structure of the apothecium. That the results in many respects are far from adequate is evident in a critical examination of his work. He himself points out at various places in his paper the unsatisfactory nature of certain of his conclusions resulting from a dearth of factual knowledge and the confusion in nomenclature of certain forms. Moreover, characters other than structure of the receptacle play an important role in his attempts to delimit the families and tribes. In his order Helotiales he reduces to six the numerous families set up by earlier authors.

Whether he is fully justified in this may be debatable, but the arrangement is perhaps a more compact and convenient organization of the great mass of poorly digested observations and classifications which plague the student of the inoperculate Discomycetes, than some others that preceded it.

One of the six groups thus set up is the family Helotiaceae. Most mycologists would doubtless place in it the genera here treated, but as Nannfeldt himself points out (p. 70) it is the most heterogeneous of his six families. It is composed of clearly divergent types not clearly bound together even by his basic criterion, apothecial structure. This unsatisfactory condition is emphasized by Nannfeldt when, in undertaking to characterize this family, he remarks (p. 71) that it is easier to recognize it than to characterize it. The disunities in the family are further emphasized when one examines his attempt to bring order into these divergent forms by applying his criterion of apothecial structure to the setting up of subfamilies or tribes. He divides the family into nine tribes. The stromatic forms fall either into the Helotioideae (*e.g. Rutstroemia, Lambertella*) or the Ciborioideae (*e.g. Sclerotinia, Monilinia, Ciboria*).

Nannfeldt's description of apothecial structures in the tribe Helotioideae appears to be based entirely on his studies of *Rutstroemia firma* and five species of *Helotium*, while in the Ciborioideae it is based on his study of but three species of *Sclerotinia, S. Curreyana, S. Vahliana*, and *S. Ficariae*. Furthermore, his contrast of apothecial structures in these two tribes does not appear to clearly distinguish them. Indeed, the number of species investigated is entirely too small. White (**1941**) in his studies in *Rutstroemia* shows clearly greater differences in apothecial structure among the species in that genus alone than Nannfeldt has marshalled to separate his tribes of the Helotiaceae. How little care and consideration he has given to his studies on the Ciborioideae is indicated by his perpetuation of the old idea that the apothecia of *Ciboria Caucus* (type of the genus) do not arise from sclerotia and the erroneous concept presented by Honey (**1928**) of a "pseudosclerotium" in *Monilinia*. One gets the impression that while Nannfeldt's work is extensive it does not provide evidence of that intensive and detailed knowledge of species and genera

requisite for preparation of a really satisfactory system of classification of the inoperculate Discomycetes. The heterogeneous character of his Helotiaceae suggests that a more intensive and detailed study of the genera and species comprising the family might well lead to breaking it into two or more groups of family rank. The studies I have made of dozens of species commonly assigned to genera in this family lead me to the conviction that the stromatic forms constitute a fairly compact and well marked group taxonomically distinct from the non-stromatic species. The bulk of the latter appear to belong in the genus *Helotium* and related genera. When intensively studied from fresh material of all their structures they may be found to constitute another family which the name Helotiaceae would properly designate.

In the past, mycologists who have devoted attention to the classification of the Discomycetes have sought for taxonomic characters almost entirely in the apothecium, on the theory that only in the so-called "perfect stage" are reliable evidences of generic, tribal, or family relationships to be found. This is an outmoded and illogical point of view. A careful and accurate evaluation of all the structures of a fungus is necessary to a sound judgment of its place in the natural system of classification.

While the members of a natural group usually exhibit in common one outstanding character which is correlated with certain less prominent features, this is not always the case. They may exhibit their natural unity by a combination of characters no one of which is necessarily common to all of them. In the group of genera here under consideration, the development of a stroma is common to all and is the most outstanding mark of their natural relationship. Moreover, all the known species have stipitate apothecia. Certain other characters less striking help delimit the family. The typically ellipsoidal form of the ascospore is an obvious family character. The species agree in general also in the shape of the spermatium. It is chiefly globose to slightly ovate, never slender rod-shaped as it is for example in the Cenangiaceae or in certain families of the Pyrenomycetes. While stromata, stipitate apothecia, ellipsoidal ascospores, and globose spermatia are not individually peculiar to the Sclerotiniaceae, their occurrence in combination sets this group off from all other inoperculate

Discomycetes. It should be emphasized, however, that not all stromatic inoperculates belong in the Sclerotiniaceae. This is illustrated by the species of the genus *Pycnopeziza* White & Whetzel (**1938**). Their cleistocarpous ascocarp and rod-shaped spermatium exclude them and seem to relate them rather closely to the Cenangiaceae.

The designation Helotiaceae or some variant of it has been used in a slightly different sense by nearly every ambitious discosystematist since it was first started on its way by Karsten (**1871**). The group has never been clearly characterized on the basis of a comprehensive and reasonably well authenticated knowledge of the forms included. It has embraced a heterogeneous collection of genera, few of which have received detailed and critical study. The monograph of *Rutstroemia* by White, the work of Honey on the genus *Monilinia,* and the studies by the author on *Lambertella, Sclerotinia,* etc. represent a start on a critical examination of the genera commonly referred to the group.

Since apparently no previous student of the inoperculate Discomycetes has conceived of the genera here assembled as constituting a distinct family it seems desirable to designate it with a new family name. The only previous approximation to my concept of the family is the tribe *Ciboriées* in the family *Ciboriaçées* of Boudier (**1907**). He, however, places the forms now regarded as species of *Rutstroemia* in his other tribe of this family, *i.e.* the *Hélotiés,* under the generic name *Phialea.* The characters on which he based his family and tribes are, moreover, quite different from those on which I here base my concept of the family Sclerotiniaceae.[2]

Family **Sclerotiniaceae** Whetzel, fam. nov.

Apothecium arising from a definite sclerotium or a stromatized portion of the substratum, stipitate, cupulate, funnel-form or saucer-shaped except in one genus where it is verpoid, *i.e.* shaped as in *Verpa,* usually brown; *ascus* inoperculate, commonly 8-spored; *ascospores* ellipsoidal, often flattened on one side, usually hyaline,

[2] The establishment of this new family under this name was first proposed by Professor Whetzel in 1943 (Lloydia **6**: 18).

unicellular and smooth; *spermatia* usually globose to slightly ovate; *conidial forms* various, in most genera lacking.

Apothecium ex sclerotio definito vel stromatita substrati parte oriundum, stipitatum, cupulatum, infundibuliforme vel patelliforme, in uno genere verpoideum, *i.e. Verpa*-forme, plerumque fuscum; ascus inoperculatus, plerumque octosporus; ascosporae ellipsoideae, saepe uno lato applanatae, plerumque hyalinae, unicellulares laevisque; spermatia plerumque globosa vel vix ovata; formae conideae variae, in plerisque generibus deficientes.

DESCRIPTION OF ORGANS AND DEFINITION OF TERMS

Preliminary to characterization of the genera of the family it seems desirable to describe certain organs and define certain terms as I apply them.

The STROMA is a food storage organ. The major portion of its body, constituting the MEDULLA, is wholly or partially enveloped by a rather sharply differentiated RIND. The stromata of the Sclerotiniaceae are of two generalized types, the *sclerotial* and the *substratal*. The *sclerotial stroma* (commonly called the *sclerotium*) has a more or less characteristic form and a strictly hyphal structure under the natural conditions of its development. While elements of the substrate may be embedded in its medulla they occur there only incidentally and do not constitute a part of the reserve food supply. The *substratal stroma* is of a diffuse or indefinite form, its medulla being composed of a loose hyphal weft or network permeating and preserving as a food supply a portion of the suscept or other substrate (*e.g.* culture media).

The sclerotial stromata both as to form and structure are of several more or less distinctive types which I designate here by new terms. The TUBEROID SCLEROTIA, characteristic of species of *Sclerotinia*, are borne free on aerial hyphae and only rarely have remnants of the suscept tissue embedded in them. They tend to be globose when formed free of external pressure. They are, however, often elongate, cylindrical, knobbed, fused, or even irregularly flattened or otherwise irregularly shaped, when formed in natural cavities of the suscept (FIGS. 1–5). The medulla, usually white, is sometimes gray and rarely pinkish. It consists of wide, densely interwoven, thick-walled hyphae, with occasional, small interhyphal spaces. The rind is composed of dark-colored

(usually brown or black), relatively thin-walled palisade cells commonly two or more layers in thickness. The dark color of the rind cells is apparently due to impregnated oxidation products of the dead protoplasmic contents. Sclerotia of this type are normally completely covered by the rind but when formed in artificial culture against the glass side of a test tube usually develop no rind over the contact surface until freed and exposed to the air. If a bit of the rind be cut away from a freshly matured sclerotium, a new rind quickly forms under normal conditions of moisture and air.

The HOLLOW SPHAEROID SCLEROTIUM, characteristic of species of *Monilinia,* is formed just beneath the cuticle in the fruit of the suscept and involves the digestion of the fleshy tissues to a considerable depth. A medulla of large, thick-walled hyphae is covered inwardly as well as outwardly by a well-defined black rind. The structure of the sclerotium is essentially that of the tuberoid type. The rotting away of the enclosed tissues leaves a more or less complete hollow sclerotial sphere of leathery or rubbery consistency (FIG. 10) which wrinkles and shrivels on drying, usually more or less tightly enclosing the seed or unrotted core of the fruit.

The MANTELOID-SPHAERULATE SCLEROTIUM, characteristic of species of *Stromatinia,* presents a unique differentiation of the stroma into two strikingly different forms, due to conditions not yet fully understood. The stroma from which the apothecia arise consists of a thin, subcuticular sclerotium manteling the rhizome or other substrate. It is structurally very similar to the tuberoid sclerotium and is accompanied by tiny black sphaerules of like structure which we have designated *sclerotules.* The latter are borne free on the mycelium and are incapable of giving rise to apothecia. Either form may be produced separately in nature. They may occur together, at least on artificial media.

The DISCOID SCLEROTIA, characteristic of species of *Ciborinia,* are usually found in the necrotized tissue of the leaf of the suscept. They are formed by digesting the tissues between the lower and upper cuticle of the leaf and replacing them with densely interwoven hyphae. These sclerotia are black, usually circular, elongate or ovate-elliptical, thin, of rather uniform thickness, flat or, on drying, somewhat concavo-convex, either persistent in the dead

leaf or dehiscent (FIGS. 6–7). Their structure is essentially that of the tuberoid sclerotia except that the medullary hyphae are more slender and have only moderately thickened walls. Remnants of indigestible vascular elements are usually to be found embedded in the medulla.

The MUMMIOID SCLEROTIA, characteristic of species of *Ciboria*, simulate the form of the stromatized organs (catkin or seed) of the affected plant (FIGS. 11–15). They are dark brown or black. Their structure is essentially that of the discoid sclerotia. They too are formed by the digestion of the suscept tissues and replacement of these with a medullary prosenchyma enclosed in a rind of fungal cells. The medullary hyphae are slender with only moderately thickened walls. Remnants of indigestible vascular elements are usually to be found embedded in the medulla. The stromata of this type usually present little of the external aspect of true sclerotia. They appear to be merely dead overwintered catkins or seeds. It is only on microscopic examination that their true sclerotial nature is seen.

The PLANO-CONVEXOID SCLEROTIA, characteristic of species of *Botryotinia* and *Streptotinia*, are usually formed on or just beneath the cuticle of the necrotized suscept and are in most cases firmly attached. They are black, flat or concave on the attachment surface and more or less erumpent, varying from hemispherical or loaf-shaped to slightly convex (FIGS. 16–24). The rind is wanting or poorly developed over the surface of attachment. The structure of the medulla is fundamentally different from that of the tuberoid type. The hyphae are relatively more slender, thinner-walled, rather loosely interwoven and embedded in a hyaline, flexible matrix. There are no interhyphal spaces. The rind is black and structurally not unlike that of the tuberoid sclerotia.

The SUBSTRATAL STROMATA are all essentially of one type in external form and internal structure. They are characteristic of species of *Rutstroemia* and *Lambertella* where they are visible on the surface of dead leaves and fruits as black patches or crusts or as irregular areas delimited by an irregular, thin, black line. This line consists of the edge view of the rind passing at right angles through the leaf or petiole, blocking off the peculiarly preserved suscept tissues which are threaded through and through with a

loose weft or network of hyaline, slender, anastomosed, thin-walled hyphae. The rind sometimes extends along the leaf surface over veins and veinlets or even spreads out here and there over the blade. Frequently, however, the cuticle itself appears to function in part as a rind. The rind is usually but one cell thick, of slender, irregular, brown- or black-walled cells, forming in surface view a pattern more or less characteristic of each genus. The process by which the fungus solidifies and preserves the enclosed portion of the substrate deserves special investigation. The enclosed tissues which evidently constitute the stored food for the subsequent development of the apothecia show little evidence of other than toxic necrotization. There is no indication of digestion or food storage in the hyphal walls or luminal protoplasm. These blocked-off portions of leaf blade, petiole, fruit, agar, etc., recall the invasion of woody tissue by certain polyporaceous fungi and their formation of a similar "black line" (Campbell, **1933**, **1934**, **1936**). The stroma in *Seaverinia* also is of the substratal type but is rudimentary or vestigial in character. In the one known species it occurs on the surface of rhizomes (FIGS. 34, 35).

In general the spermatia of the Sclerotiniaceae appear at about the time that the stroma develops. The SPERMIDIA (new term proposed to designate all types of spermatial fructification) are of three kinds, *spermodermia* (my coinage), *spermodochia*, and *spermogonia*. A SPERMODERMIUM consists of a palisade or hymenium of spermatiophores of indeterminate extent formed beneath the cuticle along and over the veins and veinlets in the necrotic areas of leaves, as in certain species of *Ciborinia* (FIG. 6), or over the surface of the developing sclerotium, as in species of *Ciboria*. The SPERMODOCHIUM is a fasciculate or tuberculate aggregation of branched spermatiophores arising usually from a single hyphal cell and borne free on the aerial mycelium. Spermodochia rarely exceed a millimeter in diameter individually but are often united into larger masses. They are usually hyaline, white or olivaceous. In certain species, as for example in *Sclerotinia Camelliae* Hansen & Thomas (**1940**), they are black. Spermatiophores may arise singly here and there on the hyphae but they are usually clustered and branched. Spermodochia in some species are produced in specialized lysigenous cavities in the substrate. The re-

sultant structure has been named by us the SPERMODOCHIDIUM (Whetzel **1943**). It does not have a distinct hyphal wall. The SPERMOGONIUM is a pycnidium-like fruit body, usually a millimeter or less in diameter, black, hemispherical or flask-shaped, formed on the surface of the stroma or adjacent to it. It consists of a distinct hyphal-walled conceptacle, the inner surface of the wall giving rise to densely packed, slender, obclavate spermatiophores. The wall is finally ruptured by increasing internal pressure of the mucilaginous mass of spermatia. In all types of spermidia the SPERMATIA are produced semi-endogenously at the tips of the spermatiophores, and tend to form chains which are strikingly evident in certain species. In *Septotinia podophyllina* Whetzel intercalary collar-like bands alternate with the spermatia in the chain, the whole enveloped in a hyaline mucilaginous sheath. When placed in water, separation of the spermatia occurs in such a manner that each carries away one of the collar-like structures as a tiny appendage at its proximal end. This intercalary structure is apparently not present in all species. The spermatia (microconidia) of the Sclerotiniaceae are globose or ovate, 1–4 μ in diameter, thin-walled, hyaline or in mass olivaceous, and each contains near its center a large, well-defined body possibly nuclear in nature (Heuberger **1934**). The spermatia are produced in immense numbers. There can no longer be any doubt that they function as male cells in the process of fertilization. The occasionally reported reproduction of certain species of the Sclerotiniaceae through the germination of these "microconidia" has never been verified by other workers.

The CONIDIDIUM (new term proposed to designate all types of conidial fructification), where present in the life history of species of the Sclerotiniaceae, is one of several types. It is wanting, or at least unknown, in nine of the fifteen genera comprising the family. It is a sporodochium in species of *Monilinia* (FIG. 8) and *Septotinia,* but may consist of scattered or clustered, erect or decumbent, simple or branched conidiophores, bearing the conidia in characteristic manner, as in *Botryotinia* (FIGS. 16, 19), *Streptotinia* (FIG. 22), *Scaverinia* (FIGS. 34, 36), and *Ovulinia.*

The APOTHECIUM is stipitate in all known species of the Sclerotiniaceae. The terminal, expanded, hymenium-bearing portion is

here called the receptacle and is typically cupulate except in one genus where its *Verpa*-like form has caused us to designate it verpoid (FIGS. 25–29). In some of the cupulate species the receptacle remains cup-shaped or funnel-form to complete maturity. In others the cup flattens out to shallow saucer-shaped or disciform, and in a few species becomes typically and pronouncedly reflexed (*e.g. Coprotinia minutula* Whetzel, **1944**). In general, species differ from each other very little in the shape of the receptacle. The cups of one species may differ greatly in size, however, from those of another, and there may be considerable variation in size within the limits of a single species. In the group as a whole the cup is characteristically small, even tiny in some forms where it may measure as little as one millimeter in diameter. This is especially true in the genera *Rutstroemia, Ciboria, Botryotinia,* and *Septotinia.* At the other extreme, as in *Sclerotinia Caricis-ampullaceae,* it may reach a diameter of as much as forty millimeters. The outer surface of the receptacle is usually smooth but may be slightly hairy or pruinose. With few exceptions the apothecium is remarkably uniform in color throughout the whole group, being usually brown, commonly some shade of vinaceous brown (Ridgway). A few species have more brightly colored apothecia, especially in the genus *Rutstroemia* where yellow or red shades occur. More rarely the apothecium is white or creamy white. The shade of color in most species varies with the amount of moisture or humidity present. Dried apothecia usually revive readily in water, regaining their natural form and approximately normal color. The color of the hymenial disc is usually of a different shade than that of the outer surface of the receptacle. In the dark-spored species of *Lambertella* and *Martinia* the color of the disc changes instantly on ascospore discharge from dark brown to nearly white. The ASCI are long clavate, the length being in general proportionate to the size of the cup. The ascus tip is thickened, and the pore-plug is usually J +, *i.e.* stains blue with iodine. The ASCOSPORES of all known species may be designated roughly as ellipsoidal, though in a few cases they perhaps more nearly approximate ovoidal or even fusiform. In many species they are somewhat inequilateral, ranging from slightly flattened or concave on one face to almost reniform. Though usually

smooth they may be adorned in various ways. They are commonly hyaline and unicellular, but in *Martinia* and *Lambertella* are brownish or olivaceous, and in some species of *Rutstroemia* are frequently 2–6-septate at late maturity. Septation occurs occasionally also in species of other genera. PARAPHYSES appear to be a structural feature of the hymenium in practically all members of the family. They are typically branched, but often so near the base as to appear simple. The branches, usually three in number, are slender, hyaline, septate, and in some species slightly thickened above. The STIPE is usually more or less concolorous with the receptacle, at least in the upper portion. It tapers toward the base and may be anchored to the substratum by tufts of rhizoidal hyphae. It is commonly smooth or pruinose. The length of the stipe varies considerably, depending on how deeply the stroma is buried. Certain species (*e.g. Coprotinia minutula* Whetzel, **1944**) seem to be naturally long-stalked.

LIFE HISTORY

Most of the Sclerotiniaceae are typically vernal in their fruiting habits. The species of *Rutstroemia* are outstandingly exceptional in developing their apothecia in late summer or autumn. Even the dark-spored species of *Lambertella,* closely related to them, all appear to be spring "bloomers."

Though the members of the family are for the most part pathogenic to the plant tissues in which they live, in general they attack only mature or declining organs such as leaves, stems, and fruits. A few species appear to be saprogens, feeding only on non-living plant substrata. As a group they may be called necrogenic saprophytes. Species in certain of the genera exhibit markedly parasitic tendencies, for example *Ciborinia bifrons* or the gynicolous species of *Ciboria.* These semiparasitic forms usually fail to grow on potato-dextrose agar or other artificial media. Though during the early stages of invasion they exhibit parasitism, taking their nutrients from the living cells, eventually they kill the tissues, effect the major part of their growth, and develop their stromata from the food supply thus made abundantly available to them. At just what point in their development spermatization takes place is known in but few cases and the female mechanism is not yet fully

understood. Homothallism appears to prevail in most if not all species of some of the genera (*Sclerotinia* and *Lambertella*) while in others (*Botryotinia* and *Stromatinia*) heterothallism seems to be the rule. The situation has been studied as yet in too few forms, however, to warrant such generalizations.

The occurrence or nonoccurrence of a conidial stage in the life history provides a basis useful in generic segregation. I have not as yet discovered a case in which this feature fails to be correlated with the type of the stroma. The conidial stage develops during or shortly after the first flush of vegetative growth, generally preceding the formation of spermatia and stromata. In certain species of *Botryotinia* and *Streptotinia* the conidiophores develop also on the overwintered sclerotia and on the vegetative mycelium of the previous season. In several species of *Botryotinia* I have often found individual sclerotia bearing apothecia and tufts of conidiophores at the same time. Such species are thus provided with two kinds of primary inoculum at the opening of the growing season.

In most if not all species successful invasion by the germtube of the conidium or ascospore appears to depend on the presence of certain nutrients or growth-promoting substances in the infection court. This was early pointed out by DeBary in the case of *Sclerotinia sclerotiorum*. These substances appear to be provided by wound extrusions, excretions of the subcuticular tissues, or glandular excretions such as those of stigmatic cells. The spores apparently do not contain sufficient stored nutrients to provide the energy necessary to affect initial access to the food materials of the suscept tissues.

The species of the Sclerotiniaceae appear to be almost entirely confined to the temperate regions of the world. They are especially abundant in the cooler reaches of the north temperate zone. Certain forms like *Martinia panamaensis*, *Lambertella Jasmini*, and *L. tropicalis* seem to be restricted to a tropical habitat, but as they are known from only a very limited number of collections this conclusion is open to question. Little search for species of the family has been made in the tropics. However, it may be emphasized that the cosmopolitan and omnivorous species *Sclerotinia sclerotiorum* has rarely been found in tropical or subtropical regions ex-

cept in high mountains or in the cooler season. Though there are not many records of the collection of species of this family in the southern hemisphere this is probably due to the fact that few mycologists, especially those interested in the Discomycetes, have collected there.

Some species of *Sclerotinia, e.g. S. sclerotiorum,* under favorable moisture conditions, invade and destroy almost any organ of their suscept. Most members of the genus, however, show a rather definite restriction to certain parts of the plant. The cypericolous and juncicolous species occur largely in the culms. Species of *Monilinia* are largely restricted to fruits, though many of them may also attack flowers, young shoots, and twigs. Species of *Ciborinia* occur almost exclusively in leaves. Though species of *Stromatinia* are pathogens of undergound stems, corms, and roots they occasionally cause lesions on foliage or aboveground stems. *Ciboria* species are definitely amenticolous, some of the species invading catkins only and others ovaries only. The members of most of the other genera, though less specific as to the plant organs attacked, are largely restricted to aboveground parts.

Most members of the family are subjected in nature to periods of drought or winter cold. They maintain themselves in a dormant or inactive condition more by means of the stroma than through possession of long-lived spores. Though under very favorable conditions of uniform dryness and temperature, the conidia, and in some cases the ascospores, remain viable for considerable periods of time, it is doubtful that they do so to any appreciable extent under the variable moisture and temperature conditions that obtain in nature.

Members of the Sclerotiniaceae live and thrive in almost all sorts of habitat, except possibly extreme desert conditions. The low temperatures of the arctic regions do not inhibit the development of some of the sedge-inhabiting species. Many forms are largely restricted to a semi-aquatic habitat, and several show interesting adaptations to it, *e.g.* the sclerotia of *Sclerotinia Duriaeana, S. sulcata,* and *S. scirpicola,* when freed by the bending or breaking over of the enclosing culm (FIG. 3), float on the water of swamp or stream and lodge on mossy hummocks or muddy banks where they fruit the following spring. The sclerotia of the *Carex-*

inhabiting species, *S. longisclerotialis,* remain enclosed in the culms when they fall over and settle to the bottom of swamp pools. Then in the spring the long-stiped apothecia push up through the water to open their tiny cups just above its surface (FIG. 5). The large sclerotia of *S. Caricis-ampullaceae* and *S. Vahliana* remain in the erect dead culms of their suscepts and send up their apothecia through the submerging waters of the swamp. Certain species of *Ciboria* develop their apothecia most abundantly on mossy hummocks or among fallen leaves in or about the margins of shallow pools where the stromata often lie immersed in the water. Many species of *Sclerotinia* and *Monilinia,* however, develop apothecia only from sclerotia buried in the soil or under ground litter or at most in water soaked moss beds. Other forms, especially species of *Rutstroemia,* appear to require little moisture for their development. In general the apothecia of species of the family are found on the ground in moist woodlands or wet swamps.

KEY TO GENERA

I. Stroma a sclerotium, of more or less definite and characteristic form.
  A. Medulla composed of densely interwoven hyphae with occasional small interhyphal spaces; hyphae not embedded in a gelatinous matrix.
    1. Stroma not of the hollow-sphaeroid type; a conidial stage wanting.
      a. Stroma not formed in the tissues of the suscept, and digesting and replacing them; consequently remnants of suscept tissues not commonly embedded in the sclerotium.
        (1) Apothecia arising from a tuberoid sclerotium which, though formed free on aerial mycelium, is sometimes enclosed in natural cavities of the suscept such as the hollow stems of perennials or the culm of sedges .....1. *Sclerotinia,* p. 664
        (2) Apothecia arising from a thin, effuse, subcuticular sclerotium covering (*i.e.* manteling) the affected portion of the suscept; small, black, globose sclerotules also formed on the aerial mycelium .....4. *Stromatinia,* p. 674
      b. Stroma formed in the tissues of the suscept, digesting the available elements and replacing them with a densely interwoven medullary prosenchyma; remnants of resistant suscept tissues commonly remaining embedded among the hyphae of the medulla.
        (1) Stroma an evident, black sclerotium of the discoid type, foliicolous.
          (*a*) Apothecium cupulate to saucer-shaped
            2. *Ciborinia,* p. 667
          (*b*) Apothecium verpoid .....9. *Verpatinia,* p. 690

(2) Stroma a sclerotium of the mummioid type, andricolous or gynicolous, simulating the shape of the stromatized organ of the suscept, usually presenting externally little of the aspect of a sclerotium .....5. *Ciboria*, p. 674

2. Stroma of the hollow-sphaeroid type; a conidial stage present; conidia borne in monilioid chains in sporodochia
3. *Monilinia*, p. 668

B. Medulla lacking interhyphal spaces; medullary hyphae embedded in a hyaline, flexible to gelatinous matrix.

1. Stroma a typical, plano-convexoid sclerotium, loaf-shaped to hemispherical, formed usually on or just beneath the cuticle or epidermis of the suscept and firmly attached to it, flat to concave on the attachment surface, with the rind poorly developed or wanting there.

a. Conidial stage present; ascospores hyaline.

(1) Conidiophore of the *Botrytis cinerea* type; branches not twisted .....6. *Botryotinia*, p. 678

(2) Conidiophore similar; the branches twisted strikingly and characteristically .....8. *Streptotinia*, p. 684

b. Conidial stage wanting; ascospores olive-brown
12. *Martinia*, p. 697

2. Stroma not a typical plano-convexoid sclerotium.

a. Stroma a definite, small, thin, circular to somewhat elongate or angular sclerotium, formed in the tissues of the suscept and digesting them more or less completely; a conidial stage present.

(1) Conidia typically one- or more-septate at maturity, elongate, apically attenuate, basally truncate ....7. *Septotinia*, p. 683

(2) Conidia large, obovoid, unicellular, with a small, basal disjunctor cell .....10. *Ovulinia*, p. 696

b. Stroma not yet observed in nature, in culture of indefinite form and extent; conidial stage wanting; species coprophilous
11. *Coprotinia*, p. 697

II. Stroma indeterminate, of the substratal type, not a definite sclerotium; medulla consisting of a stromatized portion of the substrate permeated with a loose network of narrow, branching, anastomosing, thin-walled hyphae; a thin, black rind of fungus cells delimiting the medulla at least over a portion of its surface.

A. Stromatized portion of the substrate completely blocked off by or surrounded by the rind; conidial stage wanting; ascospores brown, non-septate; spermatia globose or nearly so; spermatiophores not produced on the ascospore .....14. *Lambertella*, p. 701

B. Stromatized portion of the substrate usually less definitely delimited, sometimes rudimentary or wanting; ascospores hyaline.

1. Conidial stage wanting; spermatia broadly ellipsoidal to subglobose; spermatiophores often formed on the mature ascospore; apothecia characteristically produced in late summer or autumn, structurally complex; ascospores sometimes septate at maturity
13. *Rutstroemia*, p. 698

2. Conidial stage present; conidiophore resembling that in *Botryotinia;* conidia minutely tuberculate; apothecia produced in the spring; ascospores non-septate .....15. *Scaverinia*, p. 703

GENERIC DIAGNOSES

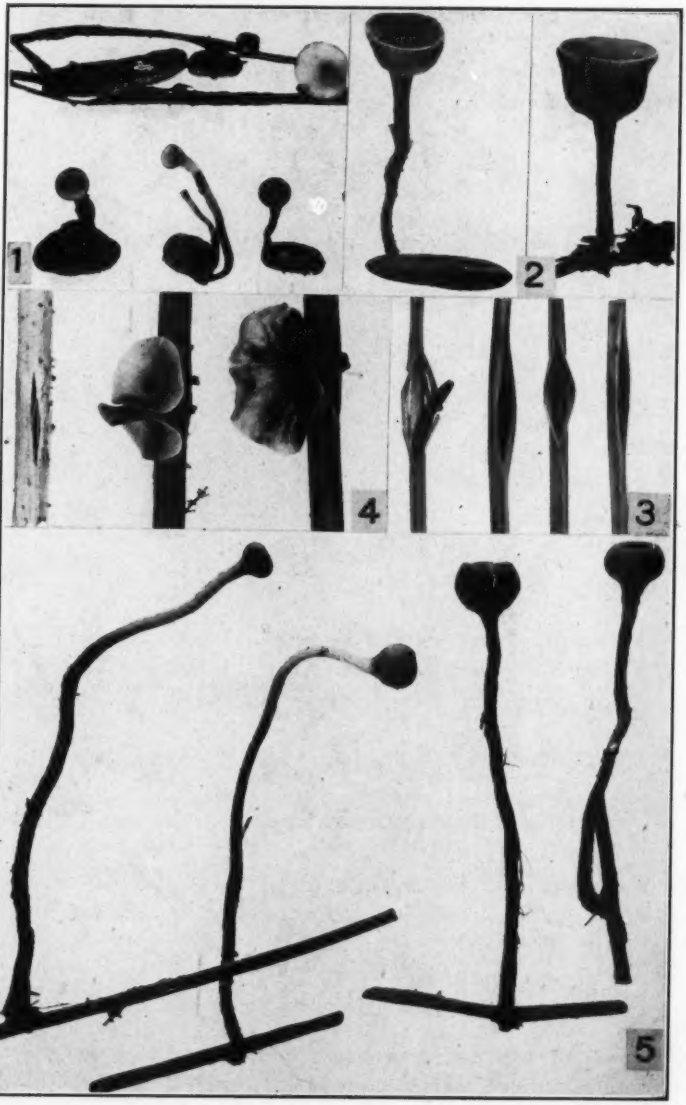
1. SCLEROTINIA Fuckel, Symb. Myc. p. 330. 1870. **(Type genus)**

(FIGS. 1–5)

Stroma a definite sclerotium of the tuberoid type, formed free on aerial hyphae and in consequence loosely attached to the substratum and tending to be globose, at most loosely enclosed in natural cavities of the suscept such as the hollow stems of perennials (FIG. 1) or the culms of sedges (FIGS. 2–5), and then often elongate, cylindrical, knobbed or even flattened or otherwise irregularly shaped; *medulla* usually white, composed of densely interwoven, broad, thick-walled, hyphal prosenchyma with occasional small interhyphal spaces; a gelatinous matrix lacking; *rind* enveloping the sclerotium completely, usually composed of two or more layers of dark-colored, thin-walled, palisade cells; *appressoria* commonly formed in culture but less profusely than in *Botryotinia; spermidium* a spermodochium, borne free and naked, or enclosed in spermodochidia, *i.e.* in specialized lysigenous cavities in the suscept tissues (Whetzel **1943**); *spermatia* globose to slightly ovate, hyaline or in mass olivaceous; *conididium* wanting; *apothecia* cupulate to funnel-form, at maturity shallow saucer-shaped to flat-expanded, some shade of brown, commonly vinaceous brown (Ridgway), 2 to 40 mm. in diameter; *ascospores* 1-celled, hyaline, ellipsoidal, inequilateral, rarely reniform.

Type species: *Sclerotinia sclerotiorum* (Lib.) DeBary, Vergl. Morph. Biol. der Pilze, Mycet. Bact. 1884.—*Syn. Peziza sclero-*

FIGS. 1–5. *Sclerotinia.* 1, *S. sclerotiorum*, type species of the type genus of the family, on *Ranunculus septentrionalis*, apothecia arising from sclerotia formed in overwintered stems, × 2 (*C15622*). 2, 3, *S. sulcata* on *Carex stricta.* 2, two three-sided sclerotia, formed in hollow culms, each bearing an apothecium, × 2 (*C11515*). 3, sclerotia in process of bursting from the culm, Nat. size (*C14747*). 4, *S. Curreyana* on *Juncus effusus*, sclerotia germinating *in situ* in hollow culms and bearing apothecia, Nat. size (*C20198*). 5, *S. longisclerotialis* on *Carex prairea*, unusually long, cylindrical sclerotia bearing apothecia, × 2 (*C11516*).



FIGS. 1–5.

tiorum Lib., Exs. No. *326, Sclerotinia Libertiana* Fuckel, Symb. Myc. p. 331. 1870.

Included species:

S. Caricis-ampullaceae Nyberg, Mem. Soc. Fauna Fl. Fenn. **10**: 20–23. 1894; see Whetzel, Mycologia **35**: 385. 1943, also Farlowia **2**: No. 3. Jan. 1946 (in press).

S. Curreyana (Berkeley) Karsten, Revisio Mònogr. p. 123. 1885.—*Syn. Peziza Curreyana* Berk., *in* Currey, Jour. Linn. Soc. **1**: 147. 1857; see Whetzel, Farlowia **2**: No. 3. Jan. 1946 (in press), also Mycologia **36**: 426. 1944.

S. Duriaeana (Tul.) Rehm, Hedwigia **21**: 66. 1882.—*Syn. Peziza Duriaeana* Tulasne, Fung. Carp. **1**: 103. 1861, and **3**: 203. 1865; see Whetzel, Mycologia **21**: 19. 1929, and **36**: 426. 1944, also Farlowia **2**: No. 3. Jan. 1946 (in press).

S. intermedia Ramsey, Phytopathology **14**: 324. 1924.

S. longisclerotialis Whetzel, Mycologia **21**: 24. 1929; see Whetzel, Farlowia **2**: No. 3. Jan. 1946 (in press).

S. minor Jagger, Jour. Agric. Res. **20**: 333. 1920.

S. Panacis Rankin, Phytopathology **2**: 30. 1912.

S. sativa Drayton & Groves, Mycologia **35**: 526. 1943.

S. scirpicola Rehm, *in* Rabenh. Krypt.-Fl. Deutschl. **1**: Abt. 3, 822. 1893; see Whetzel, Farlowia **2**: No. 3. Jan. 1946 (in press).

S. sulcata Whetzel, Mycologia **21**: 15. 1929.—*Syn. Sclerotium sulcatum* Roberge, in herb. Desmazières, Ann. Sci. Nat. III. **16**: 329. 1851; see Whetzel, Farlowia **2**: No. 3. Jan. 1946 (in press).

S. Trifoliorum Eriksson, Kongl. Landtbr. Akad. Handl. og. No. 1. p. 28–42. 1880.—*Syn. Peziza ciborioides* Hoffm., Icon. Anal. Fung. III. p. 65. 1863.

S. Vahliana Rostr., *in* Tillaeg til "Grönland Svampe (1888)." Saertryk of Meddel. om Grönland **3**: 607–608. 1891.

Two new species of *Sclerotinia* are described and a transfer to *Sclerotinia* from *Ciboria* is made in my paper (Whetzel **1946**) on cypericolous and juncicolous species.

2. **Ciborinia** Whetzel, gen. nov.[3]

(FIGS. 6, 7)

Stroma a definite sclerotium of the discoid type with black rind and white medulla, usually circular or ovate-elliptical to elongate in outline, thin, black, flat or on drying somewhat concavo-convex, foliicolous, usually erumpent and persistent, sometimes deciduous, digesting the less resistant tissues and replacing them with densely interwoven hyphae among which remnants of the resistant vascular elements of the leaf commonly remain embedded, essentially the same structurally as the tuberoid sclerotium except that the hyphae of the medulla are more slender and thinner-walled; *spermidium* a spermodermium, subcuticular along the leaf veins (FIG. 6); *spermatia* globose or ovate, hyaline, in mass pale yellowish; *conididium* wanting; *apothecia* stipitate, one to several arising from the sclerotium, cupulate to shallow saucer-shaped or flat-expanded, small to medium, 1–5 mm. in diameter, cinnamon brown to avellaneous (Ridgway), sometimes paler, rarely reddish (FIG. 7); *ascus* usually 8-spored; *ascospores* unicellular, hyaline, ellipsoidal or ovoid, usually slightly inequilateral; *paraphyses* slender, sometimes swollen at the tip.

Apothecium ex sclerotio definito oriundum, cupulatum vel subpatelliforme, parvum vel medium, cinnamomeo-fuscum vel avellaneum (Ridgway), interdum pallidius, raro rufum; sclerotium orbiculatum ovato-ellipticumve, vel

[3] Professor Whetzel had made considerable progress in the study of the species of this genus. In an unfinished manuscript he states that twelve species studied by him belong here. Eight of these form their sclerotia in the leaves of deciduous trees—poplars, willows, and maples. Four occur in the leaves of *Trillium*, *Erythronium*, and *Viola*. The apothecia of all are to be found in late spring or early summer arising from sclerotia on or about the debris of their various substrata. The as yet unpublished species bear tentative names in the herbarium at Cornell University, and the material is accompanied by photographs and notes. Some members of the genus make little or no growth on the usual sorts of culture media. Others develop readily on potato dextrose agar, where they form characteristically thin, ovate to circular, crust-like sclerotia. The mycelium in culture resembles that of *Sclerotinia* in being hyaline or in having only occasional brown hyphae, in contrast to that of *Ciboria* where the hyphae turn brown early. The apothecia in form, size, structure, color, and spore characters are indistinguishable from those of *Ciboria*, and in general are smaller than those of *Sclerotinia*. In sclerotial characters *Ciborinia* is intermediate between these genera. In lacking a conidial stage it agrees with both of them.

elongatum, tenue, nigrum, discoideum, quando siccum concavo-convexum, in folii tissibus formatum, pro illis hyphas dense intertextas substituens, indigestis resistentiorum elementorum reliquiis manentibus, plerumque erumpidum perstatumque, interdum deciduum, in structura simile sclerotii *Sclerotiniae;* medulla alba, aliquando cum intervallis interhyphas; matrix gelatinosa deficiens; spermatia in spermodermiis subcuticulariis formata; status conideus deficiens; ascosporae hyalinae, ellipsoideae vel ovatae, unicellulares, inaequilaterales.

Type species: Ciborinia bifrons (Whetzel) comb. nov.—*Syn. Sclerotium bifrons* Ellis & Ev., *in* Sacc. Syll. Fung. **14**: 1169. 1899 (*Sclerotium bifrons* Ellis & Ev., *nom. nud.* N. Am. Fungi No. 2554), *Sclerotinia bifrons* Whetzel, Mycologia **32**: 126. 1940 (not *Sclerotinia bifrons* Seaver & Shope, Mycologia **22**: 1–8. 1930), *Sclerotinia Whetzelii* Seaver, Mycologia **32**: 127. 1940; see Pomerleau, Canadian Journal of Research **18**: 199–214. 1940.

Included species:

C. Candolleana (Lév.) comb. nov.—*Syn. Peziza Candolleana* Lév., Ann. Sci. Nat. II. **20**: 233. 1843, *Sclerotinia Candolleana* (Lév.) Fuckel, Symb. Myc. p. 330. 1870.

C. confundens (Whetzel) comb. nov.—*Syn. Sclerotinia confundens* Whetzel, Mycologia **32**: 126. 1940, *S. bifrons* Seaver & Shope, Mycologia **22**: 1–8. 1930.

C. Erythronii (Whetzel) comb. nov.—*Syn. Sclerotinia Erythronii* Whetzel, Mycologia **18**: 232. *pl. 27–29. fig. 1.* 1926.

C. foliicola (Cash & Davidson) comb. nov.—*Syn. Sclerotinia foliicola* Cash & Davidson, Mycologia **25**: 269. 1933.

C. gracilis (Clements) comb. nov.—*Syn. Sclerotinia gracilis* Clements, Contrib. Bot. Dept. Univ. Nebr. n. s. **3**: 47. 1892.

3. MONILINIA Honey, Mycologia **20**: 153. 1928.

(FIGS. 8–10)

Stroma a definite sclerotium of the hollow-sphaeroid type, fructicolous, formed just beneath the cuticle, digesting the fleshy tissues

FIGS. 6, 7. *Ciborinia bifrons,* type species, on *Populus tremuloides.* 6, typical discoid sclerotia with subcuticular spermodermia along the midrib and veins, × 2 (*C14755*). 7, apothecia arising from sclerotia, Nat. size (*C11803*).

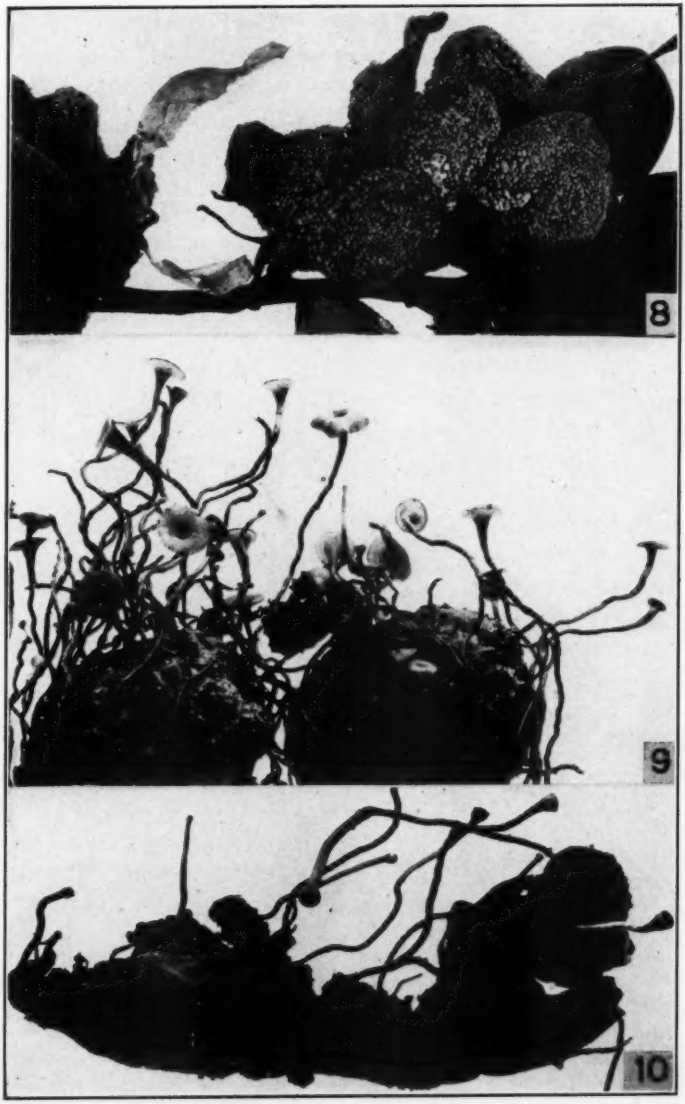
FIGS. 6, 7.

of the fruit to a considerable depth, and replacing them with a layer of broad, thick-walled, densely interwoven hyphae forming a more or less complete hollow sphere usually enclosing the core or seed (FIG. 10); this peripheral prosenchymatous layer, consisting chiefly of the medulla of the sclerotium, covered on both its inner and outer surfaces with a thin black rind; *mature sclerotium* of leathery or rubbery consistency, on drying becoming wrinkled and hard; *medulla* structurally like that of the tuberoid sclerotium; *spermidium* unknown in nature, formed as a spermodochium in culture media; *spermatia* globose or slightly ovate, hyaline; *conidiidium* a sporodochium (FIG. 8); *conidia* unicellular, ellipsoidal or lemon-shaped, formed in monilioid chains, hyaline, in mass grayish or buff, with or without disjunctors between adjacent conidia; *apothecia* funnel-form or cupulate, rarely flat-expanded (FIG. 9), some shade of brown, usually vinaceous brown (Ridgway); *asci* 8-spored, rarely 4-spored; *ascospores* unicellular, ellipsoidal, often slightly flattened on one side, hyaline.[4]

Type species: *Monilinia fructicola* (Winter) Honey, Mycologia **20**: 153. 1928.—*Syn. Ciboria fructicola* Winter, Hedwigia **22**: 131. 1883, *Sclerotinia fructicola* (Winter) Rehm, *in* Sacc. Syll. Fung. **18**: 41. 1906.

[4] Professor Whetzel mailed a copy of the portion of his manuscript dealing with *Monilinia* to Dr. E. E. Honey as soon as the first draft of it was finished. He asked him to make corrections and suggestions, and solicited his aid in checking and completing the citations given in the appended tentative list of included species. Unfortunately, Dr. Honey's reply arrived after Professor Whetzel had become too ill to give it consideration. Concerning the structure of the stroma, Dr. Honey made comments in his letter which we feel may be appropriately incorporated here. Whetzel believed Honey's conception of the stroma in *Monilinia* as a "pseudosclerotium" to be erroneous and asserted that the description and illustrations published by Honey (**1928**) "were made from immature stromata." Honey replied that his studies were based on overwintered stromata bearing apothecial fundaments. Also he said that in some species of the genus the stroma, while admittedly hollow-sphaeroid, is definitely clathrate, and in some others is actually not hollow. The following citations were given detailed consideration by Dr. Honey, and corrections made by him have been incorporated.

FIGS. 8–10. *Monilinia fructicola*. 8, sporodochia on fruit of *Prunus domestica* (cultivated blue plum), Nat. size (*C24976*). 9, overwintered fruit of *Prunus Persica* (cultivated peach) bearing apothecia, reduced (*C12602*). 10, one such fruit torn open to demonstrate the hollow-sphaeroid character of the sclerotium.



FIGS. 8–10.

Included species:

M. Amelanchieris (Reade) Honey, Mycologia **34**: 575. 1942. —*Syn. Sclerotinia Amelanchieris* Reade (based on conidial stage), Ann. Myc. **6**: 114. 1908.

M. Ariae (Schell.) comb. nov.—*Syn. Sclerotinia Ariae* Schell., Centralbl. Bakt. II. Abt. **12**: 735. 1904.

M. Aucupariae (Ludwig) comb. nov.—*Syn. Sclerotinia Aucupariae* Ludwig, *in* Woronin. Mem. Acad. Sci. St. Petersbourg VIII. **2**: No. 1. 15–20. 1895.

M. Azaleae Honey, Phytopathology **30**: 537–539. 1940.

M. baccarum (Schröt.) comb. nov.—*Syn. Rutstroemia* (*Sclerotinia*) *baccarum* Schröt., Hedwigia **18**: 180. 1879, *Sclerotinia baccarum* (Schröt.) Rehm, Hedwigia **24**: 9. 1885.

M. Corni (Reade) Honey, Amer. Jour. Bot. **23**: 105. 1936.—*Syn. Sclerotinia Corni* Reade (based on conidial stage), Ann. Myc. **6**: 113. 1908.

M. Cydoniae (Schell.) comb. nov.—*Syn. Sclerotinia Cydoniae* Schellenberg, Centralbl. Bakt. II. Abt. **17**: 189. 1907; *see* Wormald, Trans. Brit. Myc. Soc. **10**: 303–306. *pl. 18.* 1926.

M. demissa (Dana) Honey, Amer. Jour. Bot. **23**: 106. 1936.—*Syn. Sclerotinia demissa* Dana, Phytopathology **11**: 228. 1921.

M. fructigena (Aderh. & Ruhl.) Honey, Amer. Jour. Bot. **23**: 105. 1936.—*Syn. Sclerotinia fructigena* Aderh. & Ruhl., Arb. Biol. Abt. Land.-Forstw. K. Gesundheits **4**: 430. 1905.

M. Johnsonii (Ellis & Ev.) Honey, Amer. Jour. Bot. **23**: 105. 1936.—*Syn. Ciboria Johnsonii* Ellis & Everhart, Proc. Phil. Acad. Nat. Sci. **46**: 348. 1895, *Sclerotinia Crataegi* Magnus, Ber. Deutsch. Bot. Gesell. **23**: 197–202. 1905, *Sclerotinia Johnsonii* (Ellis & Ev.) Rehm, Ann. Myc. **4**: 338. 1906.

M. laxa (Aderh. & Ruhl.) Honey, Amer. Jour. Bot. **23**: 105. 1936.—*Syn. Sclerotinia Cerasi* Woronin (based on conidial stage), Mem. Acad. Sci. St. Petersbourg VII. **36**: No. 6. 39. 1888, *S. laxa* Aderhold & Ruhland, Arb. Land.- Forstw. K. Gesundheits **4**: 427. 1905, *S. cinerea* (Bonorden) Schröt. (based on conidial stage), Krypt. Fl. Schlesien **3**: 67. 1893,

S. cinerea Wormald, Ann. Bot. **35**: 131. *pl. 6, 7.* 1921, *S. cinerea* f. *Pruni* Wormald, Ann. Bot. **33**: 374. 1919 and **34**: 167. 1920; *see* Harrison, T. H. Jour. and Proc. Royal Soc. N. South Wales **67**: 132–177. 1933.

M. Ledi (Nawaschin) comb. nov.—*Syn. Sclerotinia Ledi* Nawaschin, Ber. Deut. Bot. Gesell. **12**: 117. 1894, *S. heteroica* Woronin & Nawaschin, Ber. Deut. Bot. Gesell. **12**: 187. 1894, also Zeitschrift Pflanzenk. **6**: 129–140. *pl. 3, 4.* 1896.

M. Mali (Takahashi) comb. nov.—*Syn. Sclerotinia Mali* Takahashi, Bot. Mag. Tokyo **29**: 217. 1915.

M. megalospora (Woronin) comb. nov.—*Syn. Sclerotinia megalospora* Woronin, Mem. Acad. Sci. St. Petersbourg VII. **36**: No. 6. 35–40. 1888.

M. Mespili (Schell.) comb. nov.—*Syn. Sclerotinia Mespili* Schell., Centralbl. Bakt. II. Abt. **17**: 188–196. 1907.

M. Oxycocci (Woronin) Honey, Amer. Jour. Bot. **23**: 105. 1936.—*Syn. Sclerotinia Oxycocci* Woronin, Mem. Acad. Sci. St. Petersbourg VII. **36**: No. 6. 28–30. 1888.

M. Padi (Woronin) Honey, Amer. Jour. Bot. **23**: 105. 1936.—*Syn. Sclerotinia Padi* Woronin, Mem. Acad. Sci. St. Petersbourg VIII. **2**: No. 1. 3–14. 1895, *S. angustior* Reade, Ann. Myc. **6**: 113. 1908.

M. Polycodii (Reade) Honey, Amer. Jour. Bot. **23**: 106. 1936.—*Syn. Sclerotinia Polycodii* Reade, Ann. Myc. **6**: 110. 1908.

M. Rhododendri (Fischer) comb. nov.—*Syn. Sclerotinia Rhododendri* Fischer, Ber. Schw. Bot. Gesells. **4**: 1–18. 1894.

M. Seaveri (Rehm) Honey, Amer. Jour. Bot. **23**: 105. 1936.—*Syn. Sclerotinia Seaveri* Rehm, Ann. Myc. **3**: 519. 1905.

M. Urnula (Wein.) comb. nov.—*Syn. Ciboria Urnula* Weinmann, Hymeno- Gastero-Mycetes p. 459. 1836, *Sclerotinia Vaccinii* Woronin, Mem. Acad. Sci. St. Petersbourg VII. **36**: No. 6. 3–27. 1888, *S. Urnula* (Wein.) Rehm, *in* Rabenh. Krypt.-Fl. Deutschl. **1**: Abt. 3. 804. 1893; *see* Woronin, Mem. Acad. Sci. St. Petersbourg VIII. **2**: No. 1. 4. footnote 3. 1895.

M. Vaccinii-corymbosi (Reade) Honey, Amer. Jour. Bot. **23**:

105. 1936.—*Syn. Sclerotinia Vaccinii-corymbosi* Reade, Ann. Myc. **6**: 109. 1908.

4. STROMATINIA Boudier,[5] Hist. Class. Discom. Eu. p. 108. 1907.

Stroma of the type here termed manteloid-sphaerulate, two kinds of sclerotia being formed; apothecia arising from a thin, black, subcuticular, effuse sclerotium covering or manteling the affected portion of the suscept; small, black sphaerules (*sclerotules*) borne free on the mycelium and not giving rise to apothecia; both kinds of sclerotia structurally of the tuberoid type; either sort produced separately; *sclerotules* wanting or unknown in most species under natural conditions but developing abundantly in artificial media; *spermidium* a spermodochium; *spermatia* globose; *conididium* unknown; *apothecia* resembling those of *Sclerotinia; ascospores* hyaline, unicellular.

Type species: *Stromatinia Rapulum* [Bull.] Boudier, Hist. Class. Discom. Eu. p. 108. 1907.—*Syn. Peziza Rapulum* Bull. Champ. Fr. p. 295. *pl. 485. fig. 3.* 1790.

Included species:

S. cepivorum (Berk.) Whetzel, comb. nov.—*Syn. Sclerotium cepivorum* Berk., Ann. Mag. Nat. Hist. **6**: 359. 1841.—The manteling stroma and *apothecia* are *unknown* in this species, but sclerotules are formed both in culture and under natural conditions.

S. Gladioli (Drayton) Whetzel, comb. nov.—*Syn. Sclerotinia Gladioli* (Massey) Drayton, Phytopathology **24**: 400. 1934, *Sclerotium Gladioli* Massey, Phytopathology **18**: 519–529. 1928.

S. Paridis Boudier, Hist. Class. Discom. Eu. p. 108. 1907.

S. Smilacinae Durand, Bull. Torrey Club **29**: 462. 1902.

5. CIBORIA Fuckel, Symb. Myc. p. 311. 1870.

[5] Though Professor Whetzel was attempting to bring together materials for a monographic treatment of this genus, it is clear, from an examination of his notes and correspondence, that his studies were not approaching completion. He was apparently less certain of the generic characters and limits in this case than in any other genus of the family and was in doubt concerning several species not yet adequately investigated.

(FIGS. 11–15)

Stroma a sclerotium of the mummioid type, dark brown or black, andricolous (in male catkins) or gynicolous (in seed), simulating the shape of the stromatized organ of the suscept and usually presenting externally little of the aspect of a sclerotium (FIGS. 11–15), structurally, however, essentially like the discoid sclerotium, formed by digestion of the less resistant elements of the suscept tissues and their replacement with a medullary prosenchyma enclosed in a rind of fungus cells, in culture thin, plate-like, consisting of a dark rind and a white medulla; medullary hyphae slender, with remnants of undigested vascular elements usually embedded among them; *appressoria* unknown; *spermidium* a spermodermium manteling the developing sclerotium; *spermatia* globose or ovate, hyaline or in mass faintly brownish; *conididium* wanting; *apothecia* cupulate to shallow saucer-shaped, often becoming flat-expanded or even strongly reflexed, usually some shade of brown, especially vinaceous brown (Ridgway), sometimes red or yellow, rarely white, small to medium sized, brittle waxy to tough leathery; *asci* 8-spored (rarely 4-spored); *paraphyses* hyaline or colored, filiform, slightly thickened above; *ascospores* ellipsoidal, inequilateral, unicellular, hyaline, smooth or minutely ornamented with elevations or depressions.

Type species: *Ciboria Caucus* (Reb.) Fuckel, Symb. Myc. p. 311. 1870.—*Syn. Peziza Caucus* Rebentisch, Prodr. Fl. Neomarch. p. 386. 1804.

Included species:

C. Acerina Whetzel & Buchwald, Mycologia **28**: 516. 1936.

C. Alni (Maul) comb. nov.—*Syn. Sclerotinia Alni* Maul, Hedwigia **33**: 215. 1894.

C. amentacea (Balbis) Fuckel, Symb. Myc. p. 311. 1870.—*Syn. Peziza amentacea* Balb., Mem. Acad. Turin II. p. 79. *t. 2.* 1805.

C. amenti (Batsch) comb. nov.—*Syn. Peziza amenti* Batsch, Elench. Fung. Cont. 1: 211–214. 1786, *Helotium amenti* (Batsch) Fuckel, Symb. Myc. p. 313. 1870.

C. Aschersoniana (Henn. & Plött.) comb. nov.—*Syn. Sclerotinia Aschersoniana* Hennings & Plöttner, Verh. Bot. Ver. Prov. Brandenburg **41**: 9. 1900.

C. Betulae (Woronin) White, Lloydia **4**: 171, 238. 1941.—*Syn. Sclerotinia Betulae* Woronin, *in* Nawaschin, *thesis*, St. Petersbourg, 1893.

C. carunculoides (Siegler & Jenkins) Whetzel & F. A. Wolf, Mycologia **37**: 476–491. 1945.—*Syn. Sclerotinia carunculoides* Siegler & Jenkins, Science n. s. **55**: 353. 1923, and Jour. Agric. Res. **23**: 833. 1923.

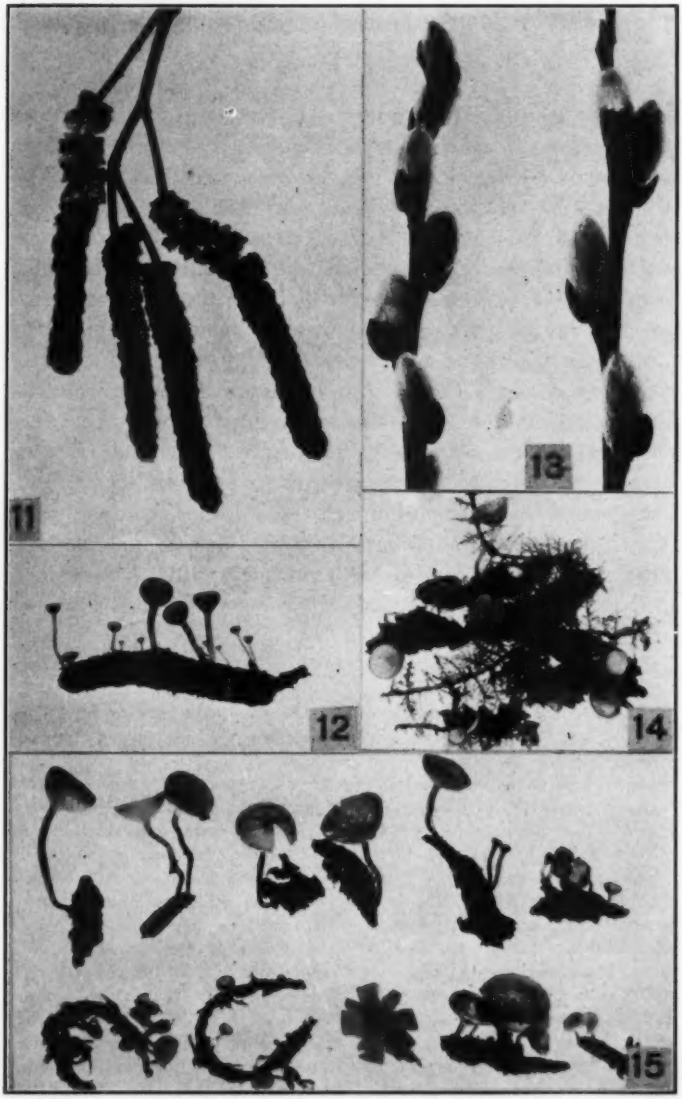
C. Carpini (Batsch) comb. nov.—*Syn. Peziza Carpini* Batsch, Elench. Fung. Cont. **1**: 215–216. 1786.

C. Coryli (Schell.) comb. nov.—*Syn. Sclerotinia Coryli* Schellenberg, Ber. Deut. Bot. Gesell. **24**: 505–511. 1905.

C. Shiraiana (Henn.) Whetzel, Mycologia **37**: 489. 1945.—*Syn. Sclerotinia Shiraiana* Hennings, *in* Engler's Jahrb. **28**: 278. 1900.[6]

[6] STATEMENT BY H. M. FITZPATRICK. The paper up to this point was written by Professor Whetzel. Here, too ill to continue, he put down his pencil. A few weeks later he died. The manuscript was his first draft, and he unquestionably intended to give it critical revision before publication. Consequently, though it is presented here largely in the form in which he prepared it, a considerable number of minor alterations have been necessary, especially in phraseology.—The remainder of the paper, beginning with the genus *Botryotinia*, has been written by me. All the footnotes are mine. Also I prepared the family diagnosis and key to genera and have inserted these above in the portion of the paper written by Whetzel. Though not a student of the taxonomy of the Discomycetes, I was more or less closely associated with him, in the Department of Plant Pathology of Cornell University, throughout all the years in which he was engaged in the study of the Sclerotiniaceae. I understood his viewpoints, terminology, and methods and was familiar with his system of filing notes, cultures, herbarium specimens, photographs, and correspondence. He was a methodical man, and his records were left in available condition. The ten generic diagnoses which follow were based by me on these records, on his statements in the preceding portion of this paper, and on his publications and those of his students. The names applied to the

FIGS. 11–15. *Ciboria*. 11, 12, *C. amentacea* on male catkins of *Alnus incana*, Nat. size (*C23366*). 11, mummification in progress five days after inoculation with shooting ascospores. 12, young apothecia developing from a mummified overwintered male catkin. 13, twigs of *Salix discolor* with normal female catkins, Nat. size. 14, 15, mummified overwintered catkins of *S. discolor* bearing apothecia of *Ciboria Caucus*, type species, Nat. size. 14, female catkins on moss-covered ground beneath the tree (*C24193*). 15, male and female catkins (*C17464*).



FIGS. 11-15.

6. **Botryotinia** Whetzel, gen. nov.

(FIGS. 16–20)

Stroma a definite black sclerotium of the type here designated plano-convexoid, characteristically flattened, loaf-shaped or hemispherical, formed usually on or just beneath the cuticle or epidermis of the suscept and firmly attached to it (FIGS. 16, 17), if covered, then in time erumpent, flat to concave on the attachment surface with the rind poorly developed or wanting there, differing thus from the tuberoid sclerotia of *Sclerotinia* which are formed free on aerial hyphae and in consequence are loosely attached to the surface of the substratum or at most are loosely enclosed in cavities of the suscept such as the hollow stems of perennials or the culms of sedges; *medulla* differing fundamentally in structure from that of the sclerotium of *Sclerotinia,* the hyphae being more slender, thinner-walled, more loosely interwoven, and embedded in a hyaline, flexible to gelatinous matrix, there being no interhyphal spaces; this structural difference clearly illustrated by DeBary (**1887**: p. 31. *fig. 13, 14*); *rind* black, distinctly differentiated, more or less definitely pseudoparenchymatous or palisade-like (FIG. 18), essentially like that in *Sclerotinia; spermidium* a spermodochium, bearing globose spermatia on branching spermatiophores, the

five new genera were selected by him. The effort has been made to complete the manuscript as far as possible in the form in which he would have written it. Though aware that he might have embodied material of which his notes give no indication, I am convinced that the paper incorporates the features that he expected to stress. As he had not yet selected illustrations, I have chosen from the files the photographs which seem most suitable. All of these, except the two used for figures 17 and 29, were made by Mr. W. R. Fisher, photographer in the Department of Plant Pathology. Throughout the years his excellent photographs have illustrated Professor Whetzel's papers. The sections of stromata, photographed for figures 28, 31, and 34, were made for my use by Mr. Bert Lear, Fellow in the Department. The Latin diagnoses were prepared, at my request, by Mrs. M. W. Allen, Scientific Assistant in the Department of Botany.—The completed manuscript was submitted for criticism to Dr. F. L. Drayton, Dr. J. Walton Groves, Dr. Edwin E. Honey, and Dr. W. Lawrence White. Most of the changes suggested by them have been made, and the paper as here published has in general their approval. We are united in a feeling of satisfaction that this summarization of Professor Whetzel's years of effort is not lost to science and will stand as a memorial to him.

entire structure enveloped in a mucilaginous matrix and drying to a waxy consistency; *conidiophores* (*Botrytis* of the *cinerea* type) erect, fasciculate, usually more or less olivaceous, often proliferating, bearing dense clusters of conidia on sterigmata on short clustered side branches which are usually hyaline and terminally swollen (FIGS. 16, 19); *conidia* smooth, unicellular, hyaline to light brown, ovate to subglobose or subpyriform, their production usually more profuse in a dry atmosphere than under conditions of high humidity; *apothecia* cupulate and stalked, some shade of brown; cup varying from infundibuliform to discoid, the margin in age sometimes reflexed (FIG. 16); *ascospores* hyaline, unicellular, ellipsoidal; *apothecial characters* essentially as in *Sclerotinia;* mycelial tips in culture on contacting the glass surface tending to branch profusely to form characteristic masses of *appressoria* which are more typical of this genus than of any other; their structure and development well illustrated by Istvánffii (**1905**).

Apothecia vere ut in *Sclerotinia;* apothecium ex sclerotio definito oriundum, stipitatum, cupulatum, fuscum; cupula infundibuliformis vel discoidea, margine interdum reflexa; ascosporae hyalinae, unicellulares, ellipsoideae; sclerotium hemisphaericum vel subhemisphaericum, plerumque ad substratum firme adnatum, haec superficie plana et cortice ibi tenue formato vel deficiente; medulla in structura ab *Sclerotinia* recedit, hyphis gracilioribus, laxius intertextis, cum septis tenuioribus, per matricem gelatinosam circumplexisque, intervallis inter hyphas deficientibus; spermatia in spermodochiis sustenta; conidiophorae ut in *Botryte cinerea;* conidia laevia unicellulares, hyalina vel subfusca, ovata vel subglobosa vel subpyriformia; apices hyphorum prominentes singularesque massas appressorium in cultura formantes.

Type species: Botryotinia convoluta (Drayton) Whetzel, comb. nov.—*Syn. Botrytis convoluta* Whetzel & Drayton, Mycologia **24**: 475. 1932, *Sclerotinia convoluta* Drayton, Mycologia **29**: 314–316. 1937.

Included species:

B. Fuckeliana (DeBary) Whetzel, comb. nov.—*Syn. Botrytis cinerea* Pers., Syn. Fung. p. 690. 1801, *Peziza Fuckeliana* DeBary, Morphol. Phys. Pilze, Flechten, Myxomyceten p. 30. 1866, *Sclerotinia Fuckeliana* (DeBary) Fuckel, Symb. Myc. p. 330. 1869.

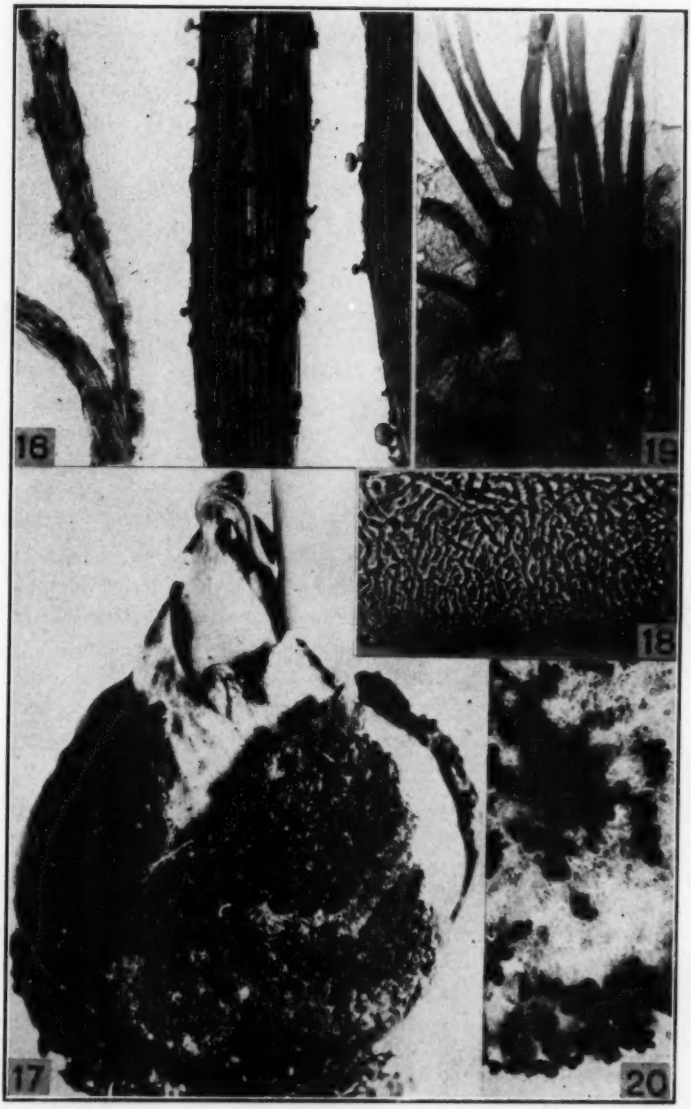
B. Porri (Beyma Thoe Kingma) Whetzel, comb. nov.—*Syn. Sclerotinia Porri* Beyma Thoe Kingma, Medel. Phytopath. Lab. Willie Commelin Scholten **10**: 43–46. 1927.

B. Ricini (Godfrey) Whetzel, comb. nov.—*Syn. Sclerotinia Ricini* Godfrey, Phytopathology **9**: 565–567. 1919.

Though many diverse conidial fungi have been placed in the form-genus *Botrytis,* Whetzel had long restricted his use of the name to the species of the so-called *cinerea* type. In addition to botryose conidiophores and conidia, these species are characterized by the possession of spermatia, appressoria, and sclerotia. Some of them have been found to form apothecia, and possibly all do so. Several have been transferred to the genus *Sclerotinia.* Convinced that they all constitute a natural group, and desiring to avoid further confusion with the form-genus *Botrytis,* Whetzel here erects the new genus *Botryotinia* for them.

Persoon described *Botrytis cinerea* from material on cabbage leaves. When Whetzel examined the type specimen it no longer contained conidia or sclerotia. As several species of *Botrytis* are commonly found on stored cabbage in Europe and America, and as Persoon's brief description is applicable to a wide range of material, it is impossible to state with certainty to what form he applied the name *B. cinerea.* It was Whetzel's practice to allude to all such fungi merely as *Botrytis* of the *cinerea* type. He emphasized that the apothecia are of little value in taxonomic separations and stated that specific identities in the group must rest primarily on characters of the conidial and sclerotial stages. The difficulties involved in attempting to define specific limits have been indicated by the results of Groves and Drayton (**1939**) in extensive cultural studies with apothecial material derived from a large number of conidial isolates.

FIGS. 16–20. *Botryotinia.* 16, *Botryotinia* sp. on *Iris versicolor,* apothecia and tufts of condiophores arising from sclerotia on overwintered leaves lying on water and wet soil, × 2 (*C29085*). 17, 18, *Botrytis* sp. on tulip (*15248*). 17, typically loaf-shaped, firmly attached sclerotia on outer bulb scales typical of *Botryotinia,* Nat. size (photo by Louise Dosdall). 18, structure of sclerotium as shown in free hand section, × 300. 19, 20, *Botryotinia convoluta,* type species, on rhizomatous iris (*C19223*). 19, base of conidiophore fascicle showing origin of conidiophores from large, dark, thick-walled, mycelial cells. 20, petri dish culture bearing typically convoluted sclerotia, Nat. size.



FIGS. 16–20.

Early in his studies of sclerotial fungi, Whetzel became much interested in the beautifully illustrated paper by Istvánffi in which *Botrytis cinerea* is treated as the conidial condition of *Sclerotinia Fuckeliana*. As a critical reading of the paper showed him that Istvánffi had not actually demonstrated the connection between the two by means of cultures, he wished especially to be able to do so. In 1930, when in Switzerland, he collected a single apothecium growing from a sclerotium attached to a grape cane, and his studies indicated that it was that of *S. Fuckeliana*. Ascospore shootings made there from it gave a culture containing conidiophores and conidia of the *B. cinerea* type. Though he felt sure that he had *S. Fuckeliana*, he realized that his data were not conclusive. Nevertheless, due to the classical character of Istvánffi's work he expected to designate *S. Fuckeliana* the type species of *Botryotinia*. The very definite element of uncertainty involved in doing so and our desire to establish the genus on an unquestionably sound basis have led us to select *S. convoluta* Drayton (**1937**) instead. Type materials of all stages of this species have been preserved, the fungus was well known to Whetzel, and it has been carefully studied, fully described, and excellently illustrated.

Whetzel had obtained cultures of *Botrytis* of the *cinerea* type from many suscepts and had collected the apothecial condition in various cases. He planned to prepare a monograph of the species of *Botryotinia* and had placed tentative names on specimens in the herbarium indicating his intention to describe a half dozen or more new species.[7]

[7] In order to avoid publication of *nomina nuda* it has been necessary to refer to Professor Whetzel's undescribed material in this fashion. In the genera not yet monographed by him he expected to erect a considerable number of new species. The specimens on which these were to be based are preserved, with associated notes and photographs, in the herbarium of the Department of Plant Pathology of Cornell University, at Ithaca, New York. His studies of the various species were all as yet more or less incomplete. Specific diagnoses had not yet been prepared by him. Probably in time his materials will be incorporated in monographic studies by other students of the Discomycetes. An attempt on our part to include descriptive matter concerning these species in this synoptical paper would in any case be inappropriate.—It was Professor Whetzel's custom to obtain each species in pure culture on agar. The resulting collection of cultures was at times large, though he made no effort to maintain a complete set embracing all the

In connection with the discussion of this genus, reference should perhaps be made to *Sclerotinia polyblastis* Gregory (**1938**). This species, based on a genetic connection between *Botrytis polyblastis* Dowson (**1928**) and apothecial material described as its perfect stage, was apparently not seen by Whetzel in the living condition. As the *Botrytis,* with large conidia reaching 60 μ in diameter, is scarcely of the *cinerea* type, and as the structure of the sclerotium was not described, inclusion of this species in *Botryotinia* could not be more than tentative. Whetzel left no statement giving an indication of his viewpoint concerning its taxonomic status.

7. SEPTOTINIA Whetzel, Mycologia **29**: 134. 1937.

Stroma a circular to elongate or angular, thin, black sclerotium, maturing in the invaded tissues of the affected plant parts usually after they have fallen to the ground, digesting the available elements of the suscept and replacing them with a densely interwoven mass of hyphae among which resistant elements such as xylem vessels commonly persist; *medulla* structurally like that of *Botryotinia,* being composed of thin-walled hyphae embedded in a transparent, gelatinous to horny matrix; *spermidium* a minute spermodochium borne on the decaying tissues at the time of sclerotium formation; *spermatium* markedly ovate instead of globose, the basal end provided with a distinct stalk or collar; the gelatinous material in which the spermatia are embedded exceptionally persistent and tending to hold them together in long chains in which the stalks have the aspect of intercalary cells; *conidial fructification* a typical sporodochium composed of massed, branching, hyaline, septate conidiophores; *conidia* hyaline, elongate, typically one- or more-septate at maturity, extremely variable in length, attenuated above and with a truncate base; *apothecia* shallow cup-shaped, stipitate, arising from overwintered sclerotia which usually have become detached from the distintegrating suscept tissue and lie free in the soil or leaf mold; *asci* slender, cylindrical; *ascospores* hyaline,

species of the family. Having published on a species, the cultures involved were ordinarily discarded. After his death his assistant transferred all of his cultures to new tubes, but it is not planned to maintain them for any considerable period. Correspondents interested in obtaining cultures should request them at once.

ovoidal, non-septate; *paraphyses* simple or branched, with swollen tips.

Type species: *Septotinia podophyllina* Whetzel, Mycologia **29**: 135. *18 fig.* 1937.—*Syn. Gloeosporium podophyllinum* Ellis & Ev., Jour. Myc. **4**: 103. 1888, *Septogloeum podophyllinum* Sacc., Syll. Fung. **10**: 497. 1892.—This species occurs in the leaves and stalks of *Podophyllum peltatum* L. and is not known on other plants. The genus, as far as known to us, is monotypic. The above generic diagnosis is based wholly on Whetzel's published account of the genus. There, the type species is fully described and abundantly illustrated.

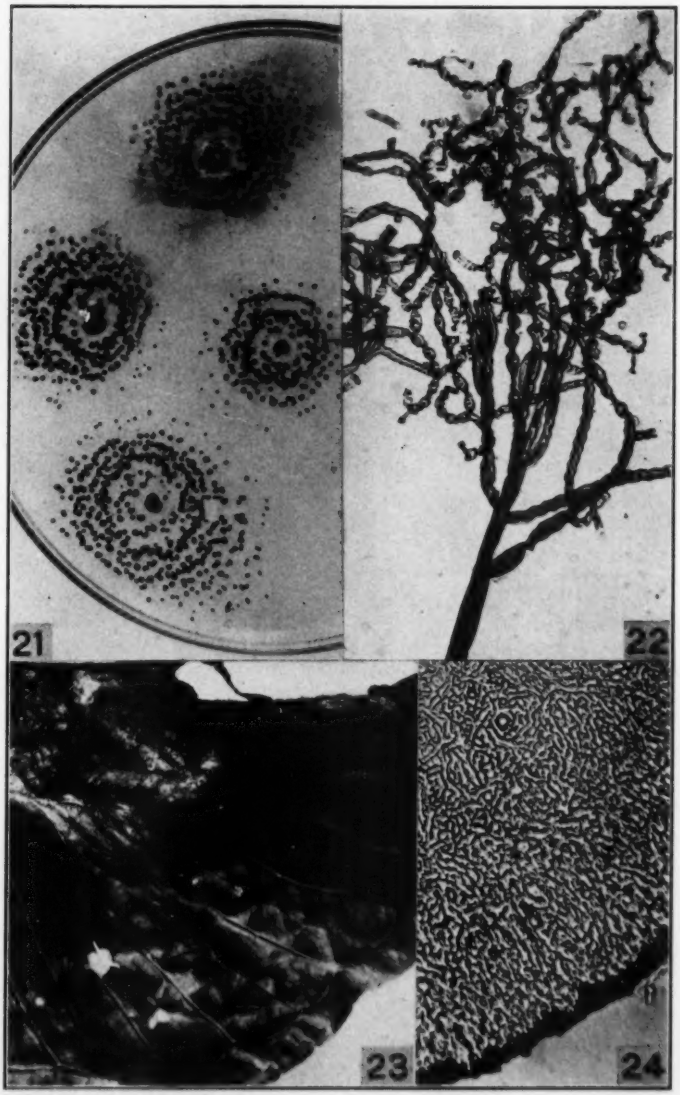
8. **Streptotinia** Whetzel, gen. nov.

(FIGS. 21–24)

Stroma a small, black sclerotium of the type here termed planoconvexoid, characteristically flattened loaf-shaped to hemispherical, firmly attached to the substrate and flat to concave on the attachment surface (FIG. 21), the rind being poorly developed or wanting there; *medulla* composed of narrow, thin-walled hyphae embedded in a hyaline, gelatinous matrix (FIG. 24); *spermatiophores* aggregated in spermodochia; *conidiophores* essentially as in *Botrytis* of the *cinerea* type except that the branches are strikingly and characteristically streptoform, *i.e.* twisted tightly as in *Streptothrix* (FIG. 22); *conidia* globose, smooth, hyaline or tinted; *apothecia* minute and short-stipitate; *ascospores* hyaline, unicellular, ellipsoidal; *generic characters* corresponding to those of *Botryotinia*, except in the streptoform nature of the branches of the conidiophore.

Apothecia sclerotiaque vere ut in *Botryotinia;* spermatia in spermodochiis sustenta; conidiophorae illarum *Botryotiniae* similes sed ramis notabile singulariterque streptoformibus, *i.e.* tortis; conidia laevia, hyalina vel leviter colorata.

FIGS. 21–24. *Streptotinia.* 21–23, *S. Arisaemae*, type species, *on Arisaema triphyllum.* 21, concentrically arranged loaf-shaped sclerotia resulting from conidial plantings on potato dextrose agar, Nat. size (*C8377 type specimen*). 22, conidiophore with typically twisted branches, × 180 (*C8377 type specimen*). 23, upper surface of leaf showing characteristic lesions, Nat. size (*C8250*). 24, *Botrytis Streptothrix on Orontium aquaticum*, structure of sclerotium as shown in free hand section, × 300 (*C3099*).

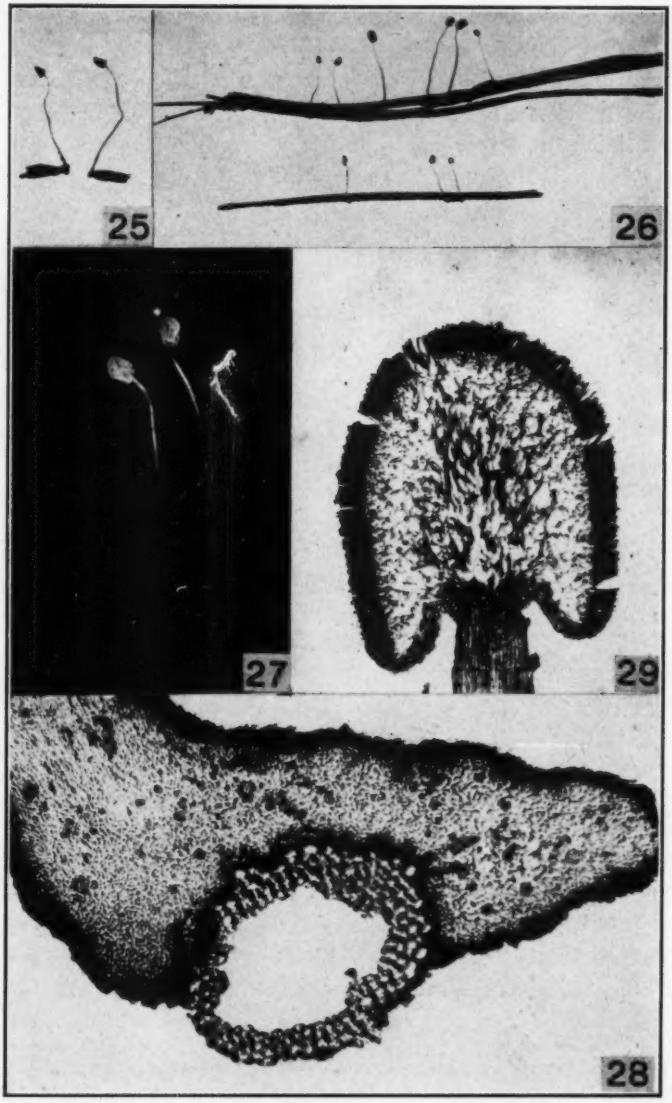


FIGS. 21–24.

Type species: Streptotinia Arisaemae Whetzel, sp. nov.—*Sclerotia* small to minute, chiefly not more than 0.5 mm. in diameter though sometimes twice that, loaf-shaped to hemispherical, smooth, shiny, round to oval or oblong or from coalescence somewhat irregular, in culture uniting rather characteristically in rows of three or more individuals but not tending to form crusts (FIG. 21); *conidiophores* scattered over the affected plant parts, arising singly or in small tufts which commonly merge to form a fluffy reddish-brown, discontinuous mat, dusty with conidia; the individual conidiophore composed of a long, slender, erect, cylindrical stalk and a rather broad, definitely terminal cluster of considerably narrower, interlacing, streptoform branches (FIG. 22); stalk about 1 mm. in length and approximately 25 μ in diameter, in reflected light noticeably iridescent; branches repeatedly forked and bearing botryose clusters of conidia on terminal branchlets; *conidia* globose, smooth, hyaline to tinted, mostly 6–7 μ in diameter; *apothecia* short-stalked, minute; the receptacle 1 mm. or less in diameter; *asci* 109–157 × 8–10 μ (mostly 130–150 × 9 μ), ascospores 8–14 × 4–6 μ (mostly 13 × 5 μ).

Sclerotia parva vel minuta, plerumque ne plus quam 0.5 mm. diametro, interdum bis tantum, subhemisphaerica vel hemisphaerica, laevia, nitida, globosa vel ovalia vel oblonga vel ex conjunctione aliquantum irregularia, haud crustas formantia; conidiophorae singulae vel in caespitibus parvis, plerumque mergentes, mattam rufo-fuscam intermittentem cum conidiis pulverulentam formantesque; singula conidiophora cum stipite longo, gracili, recto, septato, cylindracei, iridescenti, circa 1 mm. longo × 25 μ in diametro, cumque terminali aliquantum lato corymbo ramorum angustorum, tortorum, iterum iterumque furcatorum, in ramulis terminis botryoses conidiorum corymbos ferentiumque; conidia globosa, laevia, hyalina vel tingentia, plerumque 6–7 μ diametro; apothecia minuta, brevi-stipitata; cupula 1 mm.

FIGS. 25–29. *Verpatinia*. 25–28, *V. calthicola*, type species, on overwintered petioles of *Caltha palustris*. 25, long-stalked apothecia arising from detached portions of sclerotia, receptacle definitely campanulate, Nat. size (*C21996*). 26, sclerotia *in situ* giving rise to apothecia, Nat. size (*C25926 type specimen*). 27, pair of apothecia enlarged against black background to show the furrowed surface of the receptacle which in these individuals is subturbinate, × 2 (*C25926 type specimen*). 28, transverse section of long ribbon-shaped sclerotium lying lengthwise of the petiole between the cuticle and the underlying vascular bundles; sclerotium in this species avoiding incorporation of the bundles, × 85 (*C25926 type specimen*). 29, *Verpatinia* sp. collected on unidentified suscept at Tenaga, Quebec, longitudinal section of apothecial receptacle, × 120 (photo by D. B. O. Savile, loaned to us by F. L. Drayton).



FIGS. 25–29.

minusve in diametro, asci 109–157 × 8–10 μ (plerumque 130–150 × 9 μ); ascosporae 8–14 × 4–6 μ (plerumque 13 × 5 μ).

Status conideus in foliis *Arisaemae triphylli* (L.) Schott. pathogenicus, apotheciis in sclerotiis in reliquiis foliorum hibernatorum formatis.

Whetzel's records indicate that he saw apothecia representing this genus only once. On that occasion he found them arising "in great numbers from numerous minute sclerotia all together on a largely disintegrated mass of leaf debris of *Arisaema triphyllum* (L.) Schott. Conidiophore tufts also arose from the sclerotia, apparently coming on after the apothecia were nearly gone." Cultures obtained from the conidia and ascospores were identical, in both cases forming sclerotia and conidiophores with characteristically twisted branches. Whetzel says in his notes: "This connection is, therefore, sure." The collection was made, May 19, 1927, at Labrador Lake, south of Syracuse, N. Y., near the village of Apulia. Unfortunately no photographs were obtained, and the apothecia were allowed to decay. Then all the material, apothecial, conidial, and sclerotial, was discarded. The cultures in time also disappeared. Though it was Whetzel's custom to obtain photographs of petri dish cultures and to preserve dried-down cultures as herbarium specimens, he did neither in this instance. No record of the collection remains, other than that embodied by him in his notes (*C31748*).[5] In them he gives measurements of apothecia, asci, ascospores, and conidia, and we have incorporated these in the above diagnosis. He does not provide adequate descriptive matter concerning the conidial or sclerotial stages.

Diseased leaves and stalks of *Arisaema triphyllum* (FIG. 23), bearing *Botrytis* conidiophores with characteristically streptoform branches, were collected by Whetzel and his students at a half dozen different stations in Central New York during the years 1915 to 1938. At various times cultures were made, and photographs of these showing sclerotia were taken. Desiccated cultures and photographs were preserved in the herbarium along with the collections of diseased plant tissue from which the isolations were

[5] The C preceding the accession number in this and other citations in this paper designates the herbarium of the Department of Plant Pathology of Cornell University, at Ithaca, New York.

made. These specimens were all regarded by Whetzel as representing a single species, and he considered the apothecial material, above described, to be its perfect stage. He applied the names *Botrytis Arisaemae* sp. nov. and *Streptotinia Arisaemae* sp. nov. to the specimens. Our description of the conidial and sclerotial stages in the above diagnosis is based on his specimens and photographs. We have selected one of the collections (*C8377*) as the *type material*. Though Whetzel failed to preserve apothecia of the species, it should be recalled that he emphasized repeatedly that in this group of Discomycetes apothecial characters usually have little if any value in taxonomic separations.

On a considerable number of occasions Whetzel and his associates collected *Botrytis* conidiophores with streptoform branches on diseased foliage and stems of various other suscepts in the region of Ithaca, N. Y. These embrace *Caulophyllum thalictroides* (L.) Michx., *Symplocarpus foetidus* (L.) Nutt., *Stylophorum diphyllum* (Michx.) Nutt., *Glaucium flavum* Crantz, and *Dicranostigma Franchettianum* Fedde. The material was believed by Whetzel to include several additional undescribed species of *Streptotinia*, and he placed tentative specific names on some of the specimens. In various instances cultures were made, and photographs of them were taken, but apothecial material was not encountered.

Whetzel wished to designate *Botrytis Streptothrix* (Cooke & Ellis) Sacc.[9] the type species of this genus, but neither he nor any other investigator, so far as known, ever saw apothecia of the species. In June, 1919, he collected conidial material (*C3099*) at Lakehurst, New Jersey, near the type locality, on living leaves of *Orontium aquaticum* L., the suscept from which the species was originally described. Cultures were obtained and photographs of these were taken. The conidiophores and sclerotia are very similar to those of *S. Arisaemae*. Considerable additional research must be done before certainty exists as to specific identities in the genus. Whetzel realized this and had hoped to complete a monograph of the genus before undertaking the present paper.

[9] Earlier named *Polyactis Streptothrix* Cooke & Ellis, Grevillea **7**: 39. 1878, and distributed by Ellis, as N. Am. Fungi No. *130*, in the same year.

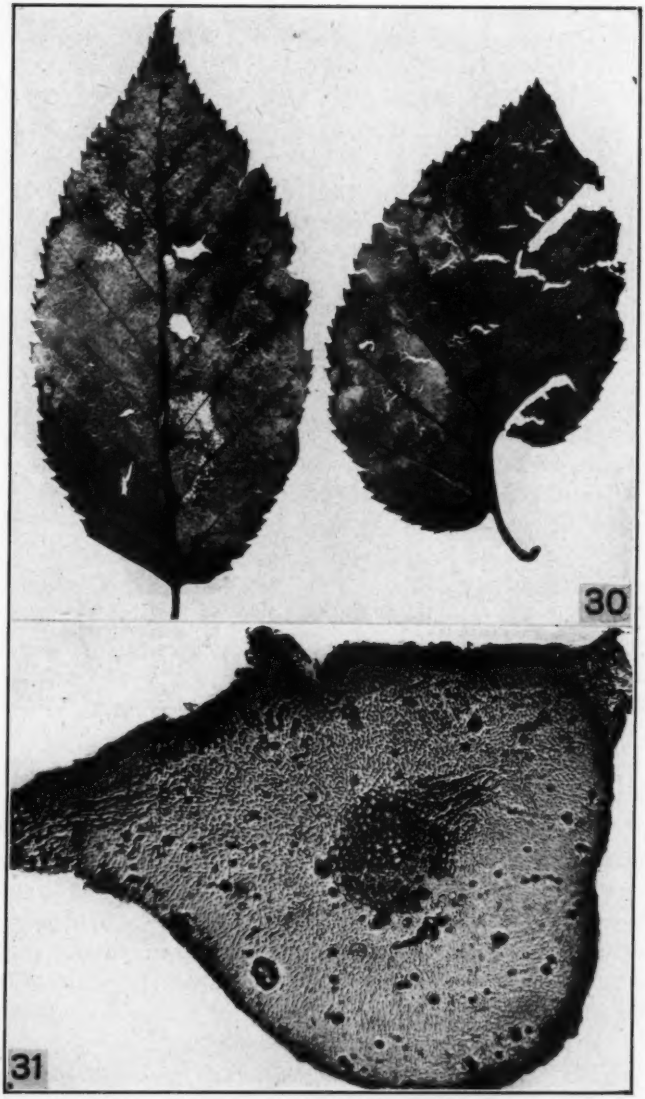
9. **Verpatinia** Whetzel & Drayton, gen. nov.

(FIGS. 25–31)

Stroma an elongate, black sclerotium of the discoid type, essentially identical with that of *Ciborinia,* foliicolous, formed beneath the cuticle, digesting the less resistant elements of the leaf tissue, and replacing them with a mass of densely interwoven hyphae, finally erumpent and more or less completely exposed but remaining partly embedded and germinating *in situ,* corresponding structurally with the tuberoid sclerotium of *Sclerotinia* but with undigested elements of the suscept tissue commonly persisting in the medulla; *rind* well differentiated and covering the sclerotium completely except at the places where undigested suscept elements such as vascular bundles protrude; *spermatia* not yet observed; *conidial stage* believed to be wanting; *apothecia* arising from the sclerotia singly or in pairs; *receptacle* characteristic, borne on a long, slender, delicate stipe and differing from that of the other genera of the family in being campanulate to cylindrical or subturbinate instead of cupulate to discoid (FIGS. 25–27); *hymenial surface* wrinkled or pitted, often more or less definitely longitudinally furrowed; tip of the stipe inserted considerably below the center of the receptacle, the margin of the latter hanging free (FIG. 29); neither stipe nor receptacle hollow, but the general form and aspect of the apothecium suggesting a tiny, long-stalked *Verpa; ascus* eight-spored, its tip thickened and staining blue with iodine; *ascospores* subbiseriate, hyaline, unicellular, ellipsoidal to fusiform, often with one side flat or slightly concave.

Stroma definitum sclerotium nigrum, in structura similis *Ciboriniae,* typice elongata, in tissibus folii formata, pro illis hyphas dense intertextas substituens, partibus elementorum resistentiorum manentibus; medulla intervallis inter hyphas dispersis, matrice gelatinosa deficiente; statibus spermatiis conideisque ignotis; receptaculum apothecii verpoideum, *i.e.* ut in *Verpa,* haud cupulatum, in stipite longo gracile sustentum; ascus octosporus, apice crasso cum iodini caeruleo tingente; ascosporae hyalinae, unicellulares, ellipsoideae vel fusiformes, saepe una parte planae vel aliquantum concavae.

FIGS. 30, 31. *Verpatinia duchesnayensis* on leaves of *Betula lutea.* 30, lower surface of leaf showing sclerotia in midrib and primary veins, Nat. size (*C28011*). 31, transverse section of sclerotium with central bundle of midrib embedded at its center; many other lesser elements of the suscept tissue especially of the palisade layer also embedded, × 85 (*C28011 type specimen*).



FIGS. 30, 31.

The apex of the columnar apothecial fundament, in its earliest stages, consists of a convex cushion bordered by an encircling roll or collar. The former is composed of tightly packed, parallel, vertical hyphae, the tips of which form the surface of the cushion and give it a papillate aspect. Their further elongation and branching results in enlargement of the end of the fundament to form the capitate, hymenium-covered receptacle. Meanwhile, the roll-like collar of bordering tissue, moving downward, becomes its pendent margin. This method of formation differs fundamentally from that of the cupulate receptacle of the other genera. Though in the genus *Coprotinia* the apothecium at maturity has the aspect of a minute, campanulate toadstool, careful observation shows the resemblance to that of *Verpatinia* to be merely superficial. The receptacle of *Coprotinia* in early stages is definitely cupulate, and the campanulate shape at maturity results from the pronounced recurving of its margin.

Type species: Verpatinia calthicola Whetzel, sp. nov.—*Sclerotium* narrow, ovate or oblong, tapering gradually to pointed ends, 3–10 mm. in length, usually about 1 mm. in width but occasionally twice that, forming a flat rather thin strip often not of uniform thickness running lengthwise in the cylinder of tissue composing the hollow petiole of the suscept and tending to avoid envelopment of its large vascular bundles (FIG. 28), either formed near the surface between the bundles and the cuticle and then at maturity so completely erumpent as to appear superficial, or lying deeper among the bundles, reaching the surface between them, and finally erumpent through one or more long slits in the tissue; persistence of undigested suscept elements in the medulla much less evident than in the following species; *exposed surface of the stroma* convex and marked by more or less prominent longitudinal striae or furrows; the opposite inner surface flat or concave; *fungus in culture* (on potato dextrose agar) forming a felty, gray, aerial, mycelial web bearing small, black, much fluted, irregular and anastomosing sclerotia; submerged mycelium brownish to black; *apothecial receptacle* campanulate to indefinitely turbinate (FIGS. 25–27), 2–3 mm. long, 1–2 mm. thick, clay color to sayal brown (Ridgway), terminating a long, slender, somewhat lighter-colored stipe; both with a tint of yellow; surface of receptacle

coarsely rugose, and marked with pits and furrows which often give a longitudinally ridged appearance (FIG. 27); *stipe* smooth, chiefly of uniform diameter throughout, sometimes swollen or flaring at the base, 5–15 mm. in length, approximately 0.5 mm. in diameter; *ascus* cylindrical in the upper spore-bearing half, tapering below very gradually to a rather broad base, 30–38 × 3–6 μ (chiefly 32 × 5–6 μ); *ascospores* ellipsoidal, with one side characteristically flat, 6–10 × 2–3 μ (chiefly 8 × 2.5 μ), becoming larger and irregular on germination, but remaining nonseptate.

Sclerotium in petiolo *Calthae palustris* L. formatum, angustum, ovatum oblongumve, acuta extrema versus gradatim conicum, plerumque circa 1 mm. latum, interdum bis tantum, 3–10 mm. longum, fasciam plana tenuem formans, saepe haud aequabiliter crassam, in longitudinem petioli in materia tubulati ejus cylindri currentem, fasces vasculares amplos haud involventem, vel prope superficiem externam inter fasces et cuticulam formatam, in statu adulto tote erumpentem per speciem externam, vel profundius inter fasces positam, superficiem inter illos per fissuras longas unas pluresve perveni-entemque; in medulla persistentis indigestis tissuum elementis multo minus manifestis quam in specie secunda; superficies proposita stromae in longitudinem sulcata striatave; receptaculum apothecii campanulatum vel indefinite turbinatum, 2–3 mm. longum, 1–2 mm. crassum, argillaceum vel sayal fuscum (Ridgway), ad apicem stipiti longi, gracilis, magis leviter colorati; superficies receptaculi crasse rugosa cum foveis sulcisque; stipes laevis, per omnes partes in diametro praecipue constans, 5–15 mm. in longitudine, circa 0.5 mm. in diametro; ascus supra cylindratus, infra conicus, 30–38 × 3–6 μ (plerumque 32 × 5–6 μ); ascosporae ellipsoideae, uno lato applanatae, 6–10 × 2–3 μ (plerumque 8 × 2.5 μ), in germinatione amplificantes irregularesque sed nonseptata manentes.

This fungus was first collected by Whetzel, May 5, 1933, in the Lloyd-Cornell Reservation, near the village of McLean, fifteen miles northeast of Ithaca, New York. The apothecia were found arising from embedded sclerotia in overwintered petioles of *Caltha palustris* L. (*C21996*). He encountered the species again on overwintered petioles of the same host, May 23, 1937, near Labrador Lake, south of Syracuse, New York. On this occasion, material was collected more abundantly, full records were made, and photographs were obtained (*C25926, type specimen*). A third collection, possibly of this species, was made only two days later, May 25, 1937, at Tenaga, Quebec, Canada, by J. W. Groves and I. L. Conners. A portion of their material was submitted to Whetzel by F. L. Drayton, but the identity of the host was not de-

termined, and there is the possibility that the Canadian specimens represent another species of the genus. The coöperation of Dr. Drayton in this connection stimulated Professor Whetzel to share authorship of the genus with his well-known student and fellow-worker in the Discomycetes.

Verpatinia duchesnayensis Whetzel, sp. nov.—*Sclerotium* elongate, at maturity as much as 25 mm. in length though often much shorter, varying from short-fusiform in early stages to long, slender-cylindrical, with rather abruptly tapering, rounded to pointed ends, dull to shiny, formed in the midrib or one of the primary veins of the leaf (FIG. 30), digesting and replacing a section of it and at maturity attaining a thickness somewhat greater than that of the normal vein, commonly erumpent on both leaf surfaces but usually remaining firmly embedded and finally germinating *in situ*, in transverse section approximately triangular (FIG. 31), composed of densely interwoven hyphae among which undigested elements of suscept tissue are much more prominent than in the preceding species, enveloping the largely unaffected vascular bundle completely except at the ends where it protrudes through the black rind into the normal vein; *upper surface* of sclerotium flat or depressed, confined to the vein, or spreading laterally to a slight extent to form a thin, black, wing-like extension beneath the upper cuticle of the leaf blade; *lower surface* rounded like that of the normal vein and similarly marked, but with more prominent longitudinal wrinkles; *fungus in culture* (on potato dextrose agar) growing slowly and forming a chocolate-brown, much convoluted, flat, sclerotial mass, several centimeters in diameter, which darkens slowly to black; *apothecia* long-stalked, arising singly or in pairs from the embedded sclerotium; *receptacle* cylindrical to barrel-shaped or turbinate, approximately 2 mm. long, 1 mm. thick, pale ashy gray, surface deeply and irregularly furrowed or wrinkled; *stipe* of uniform diameter throughout, brownish, smooth, paler above, fibrillose at the base; *ascus* slender, cylindrical in the upper spore-bearing portion, tapering gradually toward the base and rather abruptly at the tip; *hymenium* containing peculiar, thick, apically swollen, paraphysis-like elements; *ascospores* fusoidal with one side often flat or slightly concave, 9.5–12 × 3–4 μ, swelling on

germination and forming a septate mycelium which tends to break up at the septa to form oidia of various lengths.

Sclerotium elongatum, ad 25 mm. longum, saepe multo brevius, quando juvenile breve fusiform, deinde longum gracile cylindratum, in diametro abrupte diminuens rotunda acuta extrema versus, in costa vel in vena primaria folii *Betulae luteae* Michx. f. formatum, sectionem illius digerens supplantansque, in statu adulto in diametro aliquantum majus quam vena, plerumque utrimque erumpidum sed in situ firme manens germinansque, sectione transversa circa triangulare; ex hyphis dense intertextis constructum, elementis indigestis prominentioribus quam specie typa, fasci vasculari tote involuto praeterquam extrema ubi fascis per corticem protrudit et in vena normali continuat; superioris sclerotii pagina plana saepe cum alis a latere subter cuticula superiore folii extentis; inferioris sclerotii pagina rotunda venae normalis similis cum rugis longitudinalibus prominentioribus; receptaculum apothecii cylindratum vel dolioforme vel turbinatum, circa 2 mm. longum × 1 mm. crassum, pallidum cinereum, superficie profunde irregulariterque sulcata, stipite in diametro per omnes partes uniforme, subfusco, laeve, supra pallidiore ad basim fibrilloso; ascus parte ascifera cylindratus, ad apicem abrupte conicus, infra gradatim conicus; ascosporae fusoidea, uno lato planae vel aliquantum concavae, 9.5–12 × 3–4 μ, in germinatione turgentes et formantes mycelium septatum ad septa saepissime frangens oidia longitudinibus variis formansque.

The apothecia of this species were collected by Whetzel, once only, August 23, 1938, near the Forest Rangers' School at the village of Duchesnay, in County Portneuf, Quebec, Canada, on the occasion of the sixth annual summer foray of the Mycological Society of America. They were found arising from embedded sclerotia in old, disintegrating, fallen leaves of *Betula lutea* Michx. f. (*C28011, type specimens* A & B, the latter a dried-down culture). Newly-fallen leaves of this host containing wholly similar sclerotia were collected later that season, Sept. 30 and Oct. 27, at the type locality at Whetzel's request by René Pomerleau (*C28011, type specimens* C & D respectively). In notes dealing with the first of these, written Oct. 14, Whetzel says: "In most of the leaves the sclerotia appear to be only partially developed; presumably their further development and growth occur after the leaves have fallen to the ground; for the most part the leaves sent were dead and brown, having recently fallen from the trees; in one case, however, the leaf was quite green and shows a young sclerotium on the midrib apparently developing beneath the epidermis." In notes written Oct. 31, concerning the second collection he states:

"Some of the leaves show distinct lighter-brown areas in which the sclerotia are formed. Some of these involve a third or a half of the leaf surface. These lighter-colored lesions indicate that the fungus kills the leaf tissue before the leaf falls. It is obvious to me that infection occurs while the leaves are still on the trees and that development of the fungus is probably very limited and not very injurious to the leaves until about the end of the season. On the other hand the fungus apparently does not spread widely through the tissues except about the immediate point of infection. The available material suggests that it is a typical necrogen." Though some of the leaves were placed outdoors over winter, additional apothecia were not obtained from the sclerotia the following summer, and, so far as known, other collections of the species have not been made.

10. OVULINIA Weiss, Phytopathology **30**: 242. 1940.

Stroma a thin, circular to oval or irregular, shallowly cupulate, black sclerotium, formed in the invaded suscept tissues but discrete at maturity and finally falling away; *rind* sharply differentiated and covering the whole sclerotium; *medulla* corresponding structurally to that of *Botryotinia*, the hyphae being embedded in a hyaline gelatinous matrix; the invaded suscept tissue so completely digested that remnants do not persist noticeably among the medullary hyphae; *spermatia* minute, globose, usually falling apart readily, but sometimes adhering in short chains, produced at the tips of short, fusoidal spermatiophores aggregated to form minute tufts or spermodochia on the surface of the suscept; *conidia* large, obovoid, unicellular except for a basal appendage consisting of a small, sterile disjunctor cell, hyaline, borne singly at the tips of short, simple branches of the mycelium which forms a mat on the surface of the invaded suscept tissue; *apothecia* of the *Sclerotinia* type, minute, arising singly or in small groups from the edge of the sclerotium; *asci* slender, cylindrical, 8-spored; *ascospores* ellipsoidal, unicellular, hyaline, typically uniseriate; *paraphyses* chiefly unbranched, septate, terete with swollen tips.

Type species: *Ovulinia Azaleae* Weiss, Phytopathology **30**: 243. 1940.—This species forms its sclerotia in the tissue of the

corolla of cultivated azaleas and rhododendrons, causing a destructive flower blight in the southern United States. Under experimentally controlled conditions it has proved pathogenic on *Kalmia* and *Vaccinium* also. The genus, as far as known, is monotypic. The above diagnosis is based on the original publication of Weiss, and on our own examination of thin sections of sclerotia.

11. COPROTINIA Whetzel, Farlowia **1**: 484. 1944.

Stroma not yet observed in nature, as developed on potato dextrose agar of indefinite form, black, 1–2 mm. thick, differentiated into rind and medulla and in structure very similar to the sclerotium of *Botryotinia*; *rind* formed above or beneath the surface of the medium, composed of one to several layers of densely interwoven, slender hyphae, dark-brown to black; *medulla* of rather closely interwoven, slender, thin-walled hyphae embedded in a rubbery transparent matrix; *spermidia* not observed; *conidial stage* regarded as wanting; *apothecia* gregarious, some shade of brown, extremely long- and slender-stipitate; *receptacle* small, thin, at first cupulate but with the margin so strongly recurved at maturity that the appearance of a tiny toadstool is assumed; *stipe* hair-like, its surface adorned with scattered, glandular hyphal tips; *asci* very small, clavate, tapering gradually to the base; apex thickened; pore plug colored faintly blue with iodine; *ascospores* minute, slender-ellipsoidal, unicellular, hyaline; *paraphyses* cylindrical and thin-walled.

Type species: *Coprotinia minutula* Whetzel, Farlowia **1**: 484. 1944.—Collected only once on a small dung-ball of some unidentified animal at Malloryville, New York, June 22, 1942. This species and *Martinia panamaensis* Whetzel are the only known coprophilous species of the Sclerotiniaceae. The genus *Coprotinia*, as far as known, is monotypic. The above diagnosis is based wholly on Whetzel's original description.

12. MARTINIA Whetzel, Mycologia **34**: 585. 1942.

Stroma a minute, hemispherical, black sclerotium, of the planoconvexoid type, firmly attached to the substratum, flat on the attachment surface, 1–2 mm. in diameter, often fusing with neigh-

boring sclerotia to form small lobular aggregations; *rind* and *medulla* structurally as in *Botryotinia*; *spermatia* known only in culture, globose, produced from the ends of Indian-club shaped spermatiophores borne on the aerial mycelium in naked fascicles (spermodochia); *conidial stage* regarded as wanting; *apothecia* small, white, thin, membranous, fragile, rather long-stalked; *receptacle* saucer-shaped to flat-expanded; *hymenial disc* at the maturity of the ascospores olivaceous to smoky brown, becoming immediately lighter colored on spore discharge; *asci* minute, 8-spored; *ascospores* unicellular, biguttulate, ellipsoidal, olive brown; *paraphyses* few, appearing simple, but actually forked near the base, slender, cylindrical, apically almost imperceptibly enlarged.

Type species: *Martinia panamaensis* Whetzel, Mycologia **34**: 586. 1942.—This species has unusually small asci and ascospores as compared with those of species in related genera having equally small apothecia. The species is known from two collections made in Panama and the Canal Zone, in 1935 and 1937 respectively, from bark or wood of rotten logs and branches of unidentified trees. A third collection, apparently of the same species, was made in the summer of 1938 near Quebec, Canada. In this instance the apothecia developed in the laboratory from a ball of rabbit dung brought in from the open. This is especially interesting since a coprophilous tendency has been noted nowhere else in the family except in the single known collection of *Coprotinia minutula* Whetzel. The genus *Martinia* is the only member of the Sclerotiniaceae in which distinct sclerotia and brown ascospores occur together. Our treatment of this genus is based wholly on Whetzel's original description. Additional species are not known to have been described.

13. RUTSTROEMIA Karsten emend. Rehm, *in* Rabenh. Krypt.-Fl. Deutschl. **1**: Abt. III. 763. 1893; see White, W. L., Lloydia **4**: 169. 1941.

Stroma sometimes of doubtful occurrence or rudimentary, usually definitely present but indeterminate in extent and of the type here designated substratal, not a definite sclerotium, consisting of a stromatized portion of the substrate blocked off by, manteled

by, or more or less surrounded by a thin, black rind of fungus cells; *rind* thin, carbonaceous, composed of small, irregularly isodiametric cells, effuse on the surface of woody and other substrata, occurring as a thin black line or band in leaf tissues, or forming a cylinder surrounding petioles, veins, etc., always originating beneath the surface of the substrate and becoming superficial through sloughing off of the outer layer of tissue; *medulla* often indefinite in extent, but composed as in *Lambertella* of partially digested elements of the substrate threaded through and through with thin-walled, hyaline, branching hyphae; similar stromata formed in agar cultures; *spermogonia* minute, black, lenticular, solitary, subcuticular, rupturing irregularly, associated with and often adjacent to or confluent with the stroma, but always seated directly on the substrate; *spermatiophores* borne in a palisade layer on the basal wall of the spermogonium, in agar cultures arising singly from vegetative hyphae or forming a palisade layer in an acervulus-like depression in the stroma, often present in abortive form as minute tubules protruded by the ascospore at late maturity; *spermatia* broadly ellipsoidal to subglobose; *conidial stage* wanting; *apothecia* characteristically produced in late summer and early autumn, short- to long-stalked, typically brown, rarely yellow, greenish yellow, dark green, or white, firmly waxy-coriaceous, becoming hard and darker on drying, of complex structure, usually entirely prosenchymatous with a middle gelatinous zone in the ectal excipulum; *ascospores* usually large, hyaline, narrowly ellipsoidal to oblong or reniform, unicellular, sometimes becoming 2–6-celled at late maturity.

This diagnosis is based largely on that provided by White (**1941**) in his monographic treatment of this genus, but incorporates Whetzel's fundamentally different viewpoint concerning the nature of the stroma. Statements in Whetzel's notes indicate clearly that he regarded the stroma in this genus as corresponding in its essential features to that of *Lambertella* and considered the "carbonaceous black stroma" of White to be merely the rind.

White included twenty species in *Rutstroemia* and considered that they form a natural taxonomic unit. He enumerated seven characters which seemed to him the most fundamental features of the genus. No one of these is infallibly common to all the species,

a combination of any five of them being regarded by him as adequate basis for incorporation of a species in the genus. This results in a wider range and a greater diversity of form than is encountered in any other genus of the family.

Type species: *Rutstroemia firma* (Pers. ex Fries) Karsten, Bidr. Finl. Nat. Folk **19**: 108. 1871.—*Syn. Peziza firma* Pers., Syn. Fung. p. 658. 1801.

Included species:

R. americana (Durand) White, Lloydia **4**: 188. 1941.—*Syn. Ciboria americana* Durand, Bull. Torrey Club **29**: 461. 1902.

R. bolaris (Batsch ex Fries) Rehm, *in* Rabenh. Krypt.-Fl. Deutschl. **1**: Abt. 3. 765. 1893.—*Syn. Peziza bolaris* Fries, Syst. Myc. **2**: 112. 1822.

R. calopus (Fries) Rehm, *in* Rabenh. Krypt.-Fl. Deutschl. **1**: Abt. 3. 768. 1893.—*Syn. Peziza calopus* Fries, Obs. Myc. **2**: 307. 1818; Syst. Myc. **2**: 131. 1822.

R. echinophila (Bull. ex Fries) von Höhnel, Sitzungsber. Akad. Wiss. Wien, I Abt. **126**: 340. 1917.—*Syn. Peziza echinophila* Fries, Syst. Myc. **2**: 118. 1822.

R. elatina (Alb. & Schw. ex Fries) Rehm, *in* Rabenh. Krypt.-Fl. Deutschl. **1**: Abt. 3. 767. 1893.—*Syn. Peziza elatina* Fries, Syst. Myc. **2**: 112. 1822.

R. longiasca (Cavara) White, Lloydia **4**: 195. 1941.—*Syn. Pyrenopeziza longiasca* Cavara, Rev. Myc. **11**: 178. 1889.

R. longipes (Cooke & Peck) White, Lloydia **4**: 203. 1941.—*Syn. Peziza longipes* Cooke & Peck, Buffalo Soc. Nat. Sci. p. 295. March, 1875.

R. luteo-virescens (Roberge) White, Lloydia **4**: 211. 1941.—*Syn. Peziza luteo-virescens* Roberge, *in* Desmaz. Pl. Crypt. Fl. fasc. 31. No. *1541.* 1846; Ann. Sci. Nat. III. **8**: 188. 1847.

R. macrospora (Peck) Kanouse apud Wehmeyer, Canad. Jour. Res. **18**: 547. 1940.—*Syn. Helotium macrosporum* Peck, Ann. Rept. New York State Museum **26**: 82. 1874.

R. Nerii Whetzel & White, Lloydia **4**: 226. 1941.

R. nervisequa (Schröt.) White, Lloydia **4**: 223. 1941.—*Syn.*

Sclerotium nervale Alb. & Schw., Consp. Fung. p. 64. 1805, *Sclerotinia nervisequa* Schröt., Krypt.-Fl. Schl. **3**: 65. 1893.

R. petiolorum (Roberge) White, Lloydia **4**: 197. 1941.—*Syn. Peziza petiolorum* Roberge, *in* Desmaz. Pl. Crypt. Fl. ed. 1. No. *1158*. 1842; Ann. Sci. Nat. II. **17**: 96. 1842.

R. Poluninii Linder, Lloydia **4**: 224. 1941.

R. Pruni-serotinae Whetzel & White, Lloydia **4**: 219. 1941.

R. Pruni-spinosae (Libert) Whetzel & White, Lloydia **4**: 219. 1941.—*Syn. Sclerotinia Pruni-spinosae* Lib. ex Speg. & Roum., *in* Roum. Fungi Sel. Gall. Exs. No. *642*. 1880; *in* Saccardo, Michelia **2**: 328. 1881.

R. renispora (Ellis) White, Lloydia **4**: 215. 1941.—*Syn. Helotium renisporum* Ellis, *in* Cooke, Bull. Buffalo Soc. Nat. Sci. p. 299. March, 1875.

R. setulata (Dearn. & House) White, Lloydia **4**: 193. 1941.—*Syn. Ombrophila setulata* Dearn. & House, Ann. Rept. New York State Museum **1924**: 60. 1925.

R. Sydowiana (Rehm) White, Lloydia **4**: 200. 1941.—*Syn. Ombrophila Sydowiana* Rehm, *in* Sydow, Myc. March. No. *666*. 1884, *Ciboria Sydowiana* Rehm, Hedwigia **24**: 226. 1885.

R. urceolus (Fuckel) White, Lloydia **4**: 194. 1941.—*Syn. Patellaria urceolus* Fuckel, Symb. Myc. Nachtr. **2**: 54. 1873.

The above species are those placed in the genus by White. Whetzel had a manuscript in preparation in which he hoped to publish eight or ten additional species in co-authorship with White.

14. LAMBERTELLA von Höhnel, Sitz. Akad. Wiss. Wien I. Abt. **127**: 375. 1918.

Stroma diffuse, indeterminate, of the type here designated substratal, not a definite sclerotium, consisting of a stromatized portion of suscept tissue blocked off by or completely surrounded by a thin black rind of fungus cells; *rind* composed of a single layer of dark-colored, thick-walled cells which present a striking and characteristic pattern in surface view, there being a narrow translucent line between the contiguous walls of adjacent cells; *medulla* composed of partially digested suscept elements interlaced through and

through with a loose network of repeatedly branching, anastomosing, thin-walled, hyaline, septate hyphae; the fungus hyphae and suscept elements apparently enveloped together in a transparent, gelatinous matrix in which they are somehow preserved from decay until the food thus stored in the stroma is finally used in apothecial formation; *spermatia* globose to slightly elliptical, hyaline, produced successively from the tips of clavate spermatiophores borne in fasciculate naked spermodochia or in covered lenticular, black, spermogonia; *conidial stage* wanting; *apothecia* stipitate, arising from the stromatized substrate and firmly attached to it, scattered to gregarious, fleshy, elastic, becoming coriaceous or corneous on drying, reviving when moistened, usually some shade of vinaceous brown (Ridgway) or, when fresh, yellowish brown; *receptacle* cup-shaped or shallow saucer-shaped to applanate when mature; hymenial disc strikingly darker just before spore discharge, lighter immediately afterward; *stipe* relatively stout, variable in length, sometimes apparently wanting, concolorous with the receptacle, puberulent, hirsute or furfuraceous, fibrillose; *asci* usually stout-cylindrical to clavate, attenuated below, rounded to truncate and thickened at the tip which has a prominent pore plug staining blue with iodine, 8-spored; *ascospores* one-celled, broadly ellipsoidal, ovoidal, or lunate, usually flattened or concave on one face, the opposite convex wall being more or less thickened, strikingly biguttulate when young, smooth or roughened, golden brown or, when fully mature, olivaceous brown, uniseriate, tending to become biseriate before discharge; *paraphyses* two- to three-branched, slender, septate, hyaline; the terminal cell usually somewhat clavate.

In leaf-inhabiting species of the genus the stromatized block of tissue is usually delimited by a narrow black band of rind cells passing through the leaf tissues perpendicular to the surface. The rind may or may not extend partially over the surfaces of this blocked off portion. In fruit-inhabiting species the rind covers the entire surface of a thin peripheral layer or shell of stromatized suscept tissue surrounding the non-stromatized tissues of the fleshy part of the fruit and the enclosed seed. The stroma differs fundamentally in character from that of *Monilinia* where a similar peripheral stromatic shell exists but is structurally of the tuberoid type. In *Monilinia* the medulla is composed of tightly inter-

woven, thick-walled hyphae, and is covered on the inner surface as well as the outer with a fully differentiated rind. The genus *Martinia*, the only other genus of the family having colored ascospores, differs from *Lambertella* in forming a definite sclerotium. This discussion and the above diagnosis are based wholly on the statements published by Whetzel (**1943**) in his monographic treatment of this genus. There greater detail and adequate illustrations are provided.

Type species: *Lambertella Corni-maris* von Höhnel, Sitz. Akad. Wiss. Wien, I. Abt. **127**: 375. 1918.

Included species:

L. Cephalanthi Whetzel, Lloydia **6**: 47. 1943.
L. colombiana Cash & Whetzel, Lloydia **6**: 51. 1943.
L. Hicoriae Whetzel, Lloydia **6**: 33. 1943.
L. Jasmini Seaver & Whetzel, Lloydia **6**: 37. 1943.
L. Pruni Whetzel & Zeller, Lloydia **6**: 40. 1943.
L. tropicalis (Kanouse) Whetzel, Lloydia **6**: 49. 1943.—*Syn.* *Ciboria tropicalis* Kanouse, Mycologia **33**: 463. 1941.
L. Viburni Whetzel, Lloydia **6**: 43. 1943.

15. **Seaverinia** Whetzel, gen. nov.

(FIGS. 32–36)

Stroma of the type here designated substratal, poorly developed, perhaps vestigial, not a definite sclerotium, formed in the rhizome of the suscept and visible on its surface usually as a narrow black line formed of typical rind cells where the hyphal mass bursts through the peripheral cork layer, in some cases emergent over a wider, less elongate area to form a small black patch (FIG. 35); *medulla* filling a more or less superficial cavity in the suscept tissue, commonly a long, narrow, shallow crevice, and consequently appearing broadly wedge-shaped in transverse section, composed of loosely interwoven, thin-walled hyphae mixed with partially digested elements of the suscept tissue; stromatal hyphae richly connected to hyphal ramifications which are evident throughout the adjacent invaded tissue of the rhizome; this suscept tissue rotted

FIGS. 32, 33. *Seaverinia Geranii*, type species, on *Geranium maculatum*. 32, partially exposed rhizomes bearing apothecia, photographed in their natural position in the soil. 33, apothecia attached to rhizomes and roots removed from the soil, Nat. size (*C21988*).

to a dry mealy consistency and of a characteristically reddish-brown color, many of its cells retaining their form, but their walls abnormally thickened and yellowed; *spermatia* not observed; *conidial stage* placed originally in the form-genus *Botrytis* by Seaver and Horne but excluded from it by Whetzel chiefly because the conidia differ from those of *Botrytis* of the *cinerea* type in being tuberculate and because the apothecium does not arise from a true sclerotium; *conidiophores* botryose, 1 mm. or more in length, pale-brown, sparsely septate, formed in tufts on the rhizome and roots of the suscept, and under moist conditions profusely developed, bearing conidia in rather dense clusters; *conidia* unicellular, pale-brown by transmitted light, minutely but definitely tuberculate, subglobose, tapering somewhat to the point of attachment, slightly longer than broad; *apothecia* arising from the partially decayed rhizome in clusters of varying number, stipitate; the length of the stipe varying considerably and dependent in part on the depth to which the rhizome is buried; *receptacle* shallow cupulate to subdiscoid, reaching a diameter of 15 mm.; *asci* cylindrical in the spore-bearing portion, tapering above and below, 8-spored; *ascospores* hyaline, ellipsoidal, unicellular.

Stroma in typo substratea, haud sclerotium definitum, male formata, interdum vestigialis, in rhizoma *Geranii maculati* L. formata et in superficie sua manifesta plerumque per lineam angustam nigram ex cellis typicis cuticis formatam ubi massa hyphorum per corticem peripheralem perrumpet, interdum in area latiore minus elongata emergens, maculam parvam nigram formans; medulla cavum plus minusve superficiale plerumque riman longam angustam tenuem complens, propterea in sectione transversa late cuneata vel tuberculiformis, ex hyphis parietibus tenuibus laxe intertextis et ex elementis aliquatenus digestis tissuum rhizomae composita; spermatia non observata; status conideus *Botrytitis* typi *cinerei* similis sed conidia tuberculata; apothecia ex rhizomis aliquatenus putribus et plus minusve definite ex stromata oriunda, forma, modo, coloreque eorum *Sclerotiniae* vere similia, receptaculo tenui-cupulato vel subdiscoideo; asci clavaformi-cylindrati octo-sporati; ascosporae hyalinae, ellipsoideae, unicellulares.

Type species: Seaverinia Geranii (Seaver & Horne) Whetzel, comb. nov.—*Syn. Sclerotinia* (*Stromatinia*) *Geranii* Seaver & Horne, Memoirs Torrey Club **17**: 205–206. 1918.—The species is known only from the rhizomes of *Geranium maculatum* L., the type locality being the northern end of Van Cortlandt Park, New York City. It has also been found on the grounds of the New

FIGS. 34–36.

York Botanical Garden in Bronx Park. Davis (**1926**) reported its occurrence near Madison, Wisconsin. The genus, as far as known, is monotypic.

Whetzel collected the species twice, May 1, 1919 and April 22, 1927, at the type location in the company of Seaver. Later he found it on several occasions in considerable quantity in the Lloyd-Cornell Reservation at McLean, New York, near Ithaca (FIGS. 32, 33). He studied the fungus in cultures obtained from single ascospores and conidia. Definite sclerotia such as those of *Botryotinia* did not develop (FIG. 36). The above description of the stroma was based by us on his notes and photographs and on our own study of sectioned rhizomes. One of the sections examined (FIG. 34) shows the base of a tuft of conidiophores attached to the surface of the stroma. Though Whetzel was undoubtedly convinced that the stroma is that of *S. Geranii*, and presumably performed experiments demonstrating the point to his own satisfaction, we have failed to find records in his notes in this connection.

INDEX TO SPECIES

New names and combinations are in boldface, synonyms in italics

FIGS. 34–36. *Seaverinia Geranii* on *Geranium maculatum*. 34, stroma in transverse section; at the top of the photograph the base of a cluster of conidiophores arising from the rind is shown, × 85 (*C21988*). 35, stromata visible as prominent black lines and patches on the surface of the rhizome, × 3 (*C21988*). 36, original petri dish culture obtained by blowing conidia over the surface of the agar; though conidiophores cover much of the mycelium, definite sclerotia lacking, Nat. size (*C10781*).

GENERIC HOST INDEX OF SCLEROTINIACEAE LISTED IN THIS PAPER[10]

ABIES—*Rutstroemia elatina.*
ACER—*Ciboria acerina, Rutstroemia luteo-virescens, R. macrospora, R. setulata, ?R. Sydowiana.*
ALLIUM—*Botryotinia Porri, Stromatinia cepivorum.*
ALNUS—*Ciboria Alni, C. amentacea, Rutstroemia firma, R. nervisequa.*
AMELANCHIER—*Monilinia Amelanchieris, M. Johnsonii.*
APIUM—*Sclerotinia minor.*
ARISAEMA—*Streptotinia Arisaemae.*
AZALEA—*Monilinia Azaleae, Ovulinia Azaleae.*
BETULA—*Ciboria Betulae, Rutstroemia firma, R. macrospora, R. petiolorum, Verpatinia duchesnayensis.*
CALTHA—*Verpatinia calthicola.*
CAMELLIA—*Sclerotinia Camelliae.*
CAREX—*Ciboria Aschersoniana, Sclerotinia Caricis-ampullaceae, S. Duriaeana, S. longisclerotialis, S. sulcata.*
CARPINUS—*Ciboria Carpini, Rutstroemia bolaris, R. firma.*
CARYA—*Lambertella Hicoriae.*
CASTANEA—*Ciborinia Candolleana, Rutstroemia americana, R. echinophila, ?R. petiolorum.*
CEPHALANTHUS—*Lambertella Cephalanthi.*
CITHAREXYLUM—*Lambertella Jasmini.*
COCCOLOBIS—*Lambertella tropicalis.*
CORNUS—*Lambertella Corni-maris, Monilinia Corni.*
CORYLUS—*Ciboria Coryli, Rutstroemia bolaris, R. firma.*
CRATAEGUS—*Monilinia Johnsonii, Rutstroemia Pruni-spinosae.*
CROCUS—*Stromatinia Gladioli.*
CYDONIA—*Monilinia Cydoniae.*
DAUCUS—*Sclerotinia intermedia.*
EQUISETUM—*Rutstroemia Poluninii.*
ERIOBOTRYA—*Lambertella Jasmini.*
ERIOPHORUM—*Sclerotinia Vahliana.*
ERYTHRONIUM—*Ciborinia Erythronii, C. gracilis.*
FAGUS—*Rutstroemia bolaris, R. macrospora, R. petiolorum.*
FRAXINUS—*Rutstroemia macrospora, R. longipes.*
FREESIA—*Stromatinia Gladioli.*
GERANIUM—*Seaverinia Geranii.*
GLADIOLUS—*Stromatinia Gladioli.*
HUMULUS—*Rutstroemia bolaris.*
IRIS—*Botryotinia convoluta.*
JASMINUM—*Lambertella Jasmini.*
JUGLANS—*Rutstroemia macrospora.*
JUNCUS—*Sclerotinia Curreyana.*

[10] This index, submitted by Dr. J. Walton Groves for insertion in the paper, does not include the recorded suscepts of the omnivorous species, *Sclerotinia sclerotiorum*, nor does it, of course, embrace those of Whetzel's as yet unpublished new species. It should be noted too that not all the described species of the Sclerotiniaceae are listed in this paper.

KALMIA—*Ovulinia Azaleae* (artificial infection).
LACTUCA—*Sclerotinia minor.*
LAPEIROUSIA—*Stromatinia Gladioli.*
LEDUM—*Monilinia Ledi.*
LIGUSTRUM—*Rutstroemia Pruni-spinosae.*
MELILOTUS—*Sclerotinia sativa.*
MESPILUM—*Monilinia Mespili.*
MORUS—*Ciboria carunculoides, C. Shiraiana.*
MYRICA—*Ciboria acerina.*
NARCISSUS—*Sclerotinia sativa.*
NERIUM—*Rutstroemia Nerii.*
NYSSA—*Rutstroemia macrospora, R. renispora.*
OSTRYA—*Ciboria acerina.*
PANAX—*Sclerotinia Panacis, Stromatinia Smilacinae.*
PARIS—*Stromatinia Paridis.*
PLATANUS—*Rutstroemia luteo-virescens.*
POA—*Rutstroemia calopus.*
PODOPHYLLUM—*Septotinia podophyllina.*
POLYCODIUM—*Monilinia Polycodii.*
POPULUS—*Ciboria Caucus, Ciborinia bifrons, C. confundens, Rutstroemia firma, R. nervisequa.*
PRUNUS—*Lambertella Pruni, Monilinia demissa, M. fructicola, M. fructigena, M. laxa, M. Padi, M. Seaveri, Rutstroemia Pruni-serotinae, R. Pruni-spinosae.*
PYRUS—*Monilinia Johnsonii, M. megalospora.*
QUERCUS—*Ciborinia Candolleana, Rutstroemia bolaris, R. echinophila, R. firma, R. macrospora, R. petiolorum, R. Sydowiana.*
RHODODENDRON—*Monilinia Azaleae, M. Rhododendri, Ovulinia Azaleae.*
RIBES—*Rutstroemia firma.*
RICINUS—*Botryotinia Ricini.*
ROSA—*Rutstroemia longiasca.*
RUBUS—*Rutstroemia firma, R. urceolus.*
SALIX—*Ciboria acerina, C. amentacea, C. amenti, C. Caucus, Ciborinia foliicola, Rutstroemia bolaris.*
SCIRPUS—*Sclerotinia scirpicola.*
SMILACINA—*Stromatinia Smilacinae.*
SORBUS—*Monilinia Ariae.*
TILIA—*Rutstroemia luteo-virescens.*
TRAGOPOGON—*Sclerotinia intermedia.*
TRIFOLIUM—*Sclerotinia Trifoliorum.*
TRITONIA—*Stromatinia Gladioli.*
TSUGA—*?Rutstroemia elatina.*
TULIPA—*Sclerotinia sativa.*
ULMUS—*Rutstroemia firma.*
VACCINIUM—*Monilinia baccarum, M. Ledi, M. megalospora, M. Oxycocci, M. Urnula, M. Vaccinii-corymbosi, Ovulinia Azaleae* (artificial infection).
VIBURNUM—*Lambertella Viburni.*
VITIS—*Sclerotinia Fuckeliana.*

MISCELLANEOUS SUBSTRATA

DUNG—*Coprotinia minutula, Martinia panamaensis.*
GROUND—*Stromatinia Rapulum.*
NUT—*Lambertella columbiana.*
WOOD—*Martinia panamaensis.*

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SPECIES OF SYNCHYTRIUM IN LOUISIANA. III. THE DEVELOPMENT AND STRUCTURE OF THE GALLS

MELVILLE T. COOK

(WITH 12 FIGURES)

The fungi belonging to this genus consist, in the vegetative stage, of a single cell, living as a parasite in a single cell of a higher plant. The infections so far as known are by means of zoöspores, and are in cells that are not fully mature but cells of slightly different ages in the same leaf may be infected. After infection the fungus grows rapidly, the host cell enlarges, and usually a gall is formed by the growth of the surrounding host cells. The zoöspores are transparent and so small that they are easily overlooked. After the zoospores penetrate the host cell the fungus grows, becomes pale yellow, then deep yellow, and finally in some species orange or red. The fungus has a very large nucleus but this will not be discussed in this paper. The wall which forms around the fungus very early consists, in many and possibly all species, of three layers; the inner and middle layers are formed by the fungus, while the outer is formed from the disintegrating contents of the host cell. The thickness of the wall varies in different species and with age. It is usually thin at maturity. The inner and middle layers may be so closely united that it is difficult to determine whether there are one or two layers. The outer layer may be prominent or reduced to a few granules. The fungus grows to full size and then segments by the formation of septa which originate at the periphery, grow inward and separate the body into sporangia. The number of sporangia formed from a single infection is variable and of very little value in descriptions and for determination of species. Pronounced variations in number and size may be found in a single infected leaf. Each sporangium contains a single nucleus which divides into many, each becoming the center of a zoöspore. In some species there appears to be a single generation; the sporangia

persisting in some unknown manner until the following year when the zoöspores appear and infect young plants. Other species have several generations, each producing zoöspores that infect plants and then a generation which carries the plant to the following year.

The life histories of a few species have been studied but very little attention has been given to the structures of the galls in which the fungi develop. These gall structures appear to be more characteristic and more satisfactory for determinations and descriptions than the characters of the fungi. It is the purpose of this paper to describe the structure and development of these galls, although some attention will be given to the development of the fungi. The infections in all species described in this paper are in the epidermal cells, mostly in the leaves before they are fully developed. A few workers have reported sub-epidermal infections but some of these records are doubtful. The infected host cell grows rapidly and in most cases is almost or completely filled by the fungus early in its development. The relative sizes of fungus and host cell depend on age. The nucleus of the infected cell persists for a time but disappears before the formation of the sporangia; the protoplasm undergoes disintegration, some of it going to the formation of the outer layer of the wall around the fungus, which is abundant in some species and sparse in other species.

The fungus stimulates the growth of the cell in which it lives and also some of the surrounding cells of the host plant. The epidermal cells in contact with the infected cell grow in such a manner as to partly or completely cover it, depending on the species of the fungus. In some species the other surrounding host cells, especially those in contact with the infected cell, also grow and form a definite and characteristic sheath. These growths of the host cells result in the formation of a gall with distinctive characters by which the species of the fungus can be determined. In most species the gall is partly submerged in the tissues of the host; in some few species it is completely embedded and in other species rests on the surface of the host plant. Although the infected cell may be partly or completely embedded in the tissues of the host plant, the infections in all the species reported in this paper occur in epidermal cells. The forms and structures of the galls are characteristic of the species causing them. The galls of most species are colored,

mostly light green or pale yellow, but a few have very bright colors. These colors are in the liquid contents of the surrounding uninfected host cells.

Galls are simple (*i.e.* single) or compound (*i.e.* aggregated into groups). The compound galls may result from over-crowding or from the infection of the epidermal cells of an older gall. Although the simple galls have definite forms, they may be modified as a result of being located on different organs of the plant, or to over-crowding or possibly to other causes.

These studies start with the early infections of epidermal cells of the host plant. Very little attention has been given to sexuality of the fungi or methods of infection. The infections of the host plants by all the species reported in this paper occur in epidermal cells which are not fully mature. Most species infect cells of more or less the same age but there are some exceptions. In some cases host cells of different ages in the same leaf are infected. Host cells are sometimes infected by two or more fungi of the same species; fungi in these multiple infections are usually the same age but there are some exceptions.

The contents of the infected host cell in most species studied is much more abundant and much denser than that of the surrounding cells but undergoes pronounced changes very rapidly. It may have a vacuolate, foamy appearance at first, gradually becoming dense, disintegrates and almost disappears in some species but persists in others. It may completely fill the space between the wall of the fungus and the wall of the host cell or it may divide into two layers, one clinging to the fungus to form the third or outer layer around the fungus, while the other part clings to the wall of the host cell. In some species the fungus wall is hard and brittle and breaks easily. In some species the disintegrating contents of the infected cell is granular and gives the wall around the fungus a warty appearance. The nucleus of the infected host cell stains deeply, enlarges at first, usually clings to the fungus but finally disappears when the fungus is about one-half full size. In some species it is very difficult to demonstrate its presence.

The fungus, in some species reported in this paper, enlarges very rapidly and completely fills the host cell while in other species it enlarges much more slowly and never completely fills the host cell.

In some species the host cell is filled very early in its development and then grows much faster than the fungus, so that in later stages it is not filled by the fungus.

The fungus is a uninucleate thallus and is usually called a prosorus previous to segmentation. The nucleus and nucleolus are exceptionally large at first, but lose their identity as the fungus approaches maturity. Two or more fungi are found frequently in a single host cell; they may be the same or different ages as shown by their development. These multiple infections are much more frequent in some species than in others. Two nuclei may occur in a single fungus but the writer is uncertain whether this is the result of division or the union of two fungi in the cell; however, it appears to be the latter.

Although the characters of the fungi have been considered most important for classification of species of *Synchytrium*, the author believes that the structures of the galls are much more reliable. In this connection it should be remembered that the characters of the fungi in collections of any species of *Synchytrium* made at different times may vary. The measurements of the fungus and number of sporangia are variable and the colors vary with age. Some species of this genus, so far as known, attack a single species of host plants, while others attack several species. Cross inoculations give the only positive evidence of inter-host relationships but this has been used in the study of very few species.

The descriptions in this paper are based on thousands of sections made from freshly collected material. No effort has been made to illustrate the entire life history of any species but all species reported in this paper have been studied by the author.

SYNCHYTRIUM ERIGERONTIS Cook on *Erigeron philadelphicus* L. (FIG. 1, A–D).

This species causes the infected cells to enlarge and almost fills them at all stages of its growth (A–C). The disintegrating contents of the host cell is prominent but the nucleus is inconspicuous. Multiple infections are common but rarely more than two fungi in a cell (D). When two are present, they are usually hemispherical. The wall around the fungus forms early, is thick and appears to be made up of three layers; the inner layer is thin, the middle layer

thick, and the outer layer composed of the disintegrating material of the host cell.

In cases of severe infections the leaves are thickened. The infected cells enlarge and in some instances may extend from one to

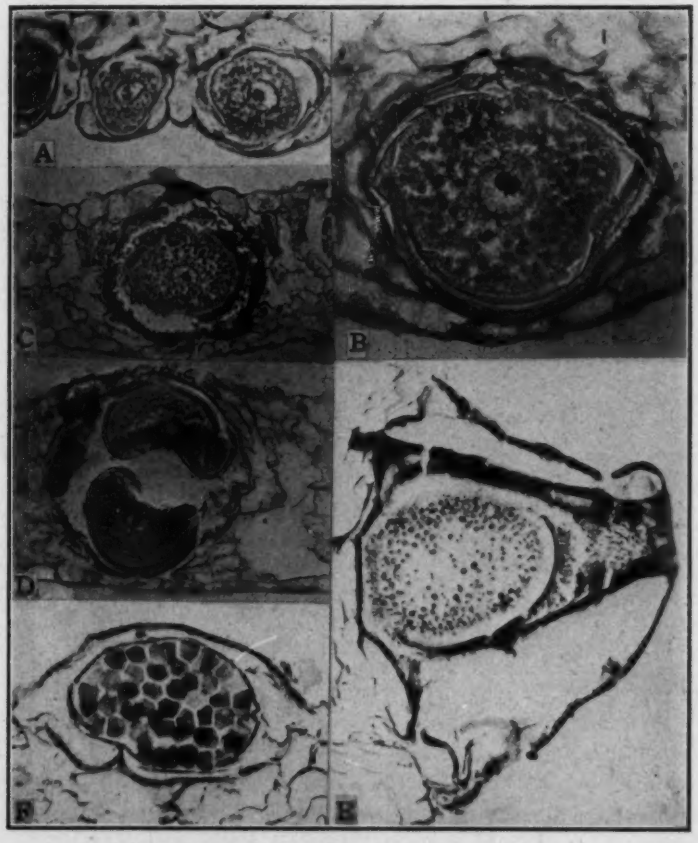

FIG. 1.

the other epidermal layer with very slight or no projections on the surfaces of the leaves and with very little or no modifications of the host tissues other than the epidermal cells in contact with the infected cell (C). In other cases the infected cell may extend only

part way through the leaf, the outer portion being covered with a layer of host cells so as to form a very simple, inconspicuous gall. Galls are more pronounced when over veins than in other places. The opening to the infected cell is small but always visible in properly cut sections. The host cells in contact with the infected cells are modified very slightly.

SYNCHYTRIUM GLOBOSUM Schröter on *Veronica perigrina* L. (FIG. 1, E, F).

In this species the fungus grows rapidly. More than one fungus in a host cell is rare. The wall around the fungus forms early, is thick at first but becomes thin with age (E, F) and is composed of three layers. The disintegrating contents of the infected host cell is usually conspicuous, especially in the outer part of the infected cell (E), but disappears almost completely (E, F) with age. In sections examined the nucleus of the infected host cell was rarely seen.

The infected cell becomes conical with the fungus in the basal part (E). The outer part of the infected cell is tubular and filled with the degenerating contents (E). The gall is conical and is composed of a few large, thin-walled cells (E). The basal parts of the leaf galls are embedded in the host tissues; the basal parts of the stem galls are embedded in the cortex but not as deep as the leaf galls.

SYNCHYTRIUM LYTHRI Cook on *Lythrum alatum* Pursh. (FIG. 2, A–E).

The fungus rarely fills the infected cell (A–D) except when very young but may do so in some cases. The disintegrating contents of the host cell may be inconspicuous or prominent. The wall around the fungus forms early, is usually thin and appears to be composed of three layers. The outer layer may be inconspicuous or rather prominent in some cases. The host cell nucleus may or may not be prominent (E).

The infected leaves usually become thickened (A), the infected cells become conical or pear-shaped and are embedded in the thickened host tissues (C, D). The host tissues grow to such an ex-

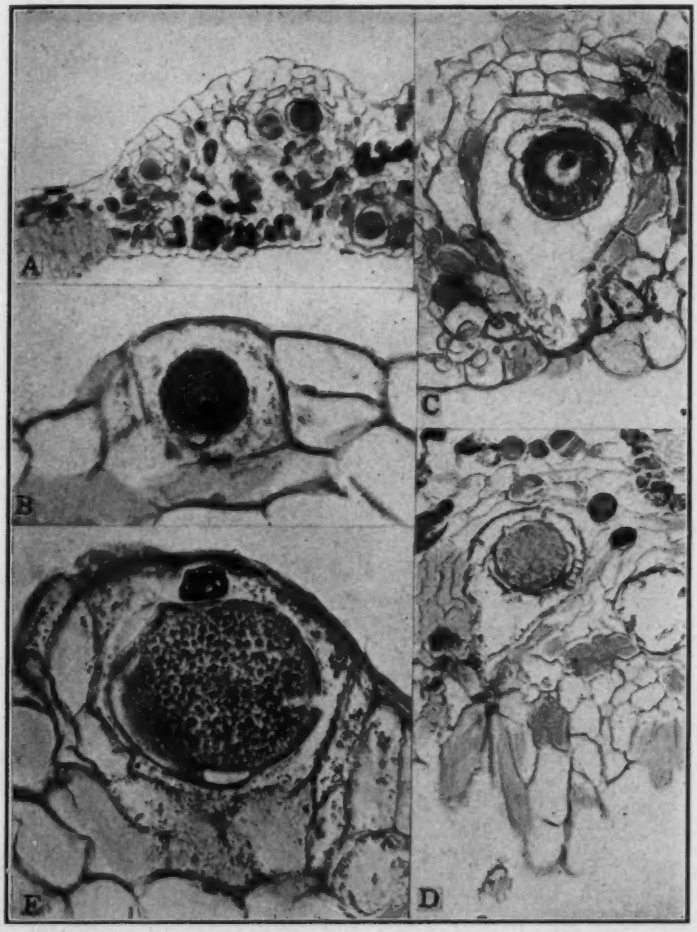

FIG. 2.

tent that the infected cells are deeply embedded (D) but the line where the cells have united over an infected cell can be traced in galls that have been cut properly (D). A very definite sheath is formed around the infected cell (C, D).

SYNCHYTRIUM FULGENS Schröter on *Oenothera laciniata* Hill (FIG. 3, A–D).

This species attacks plants of different ages in the same leaf. The fungus almost completely fills the enlarged host cell very soon after infection (A, B). Large and small fungi are frequently found in adjoining host cells indicating that infections of these cells have not occurred at the same time. Multiple infections are frequent. The disintegrating contents of the host cells are not abundant. The host cell nuclei are inconspicuous and rarely seen. The wall around the fungus forms early and may be very thin or very thick but becomes thin with age. In the material studied by the writer the wall was thin and appeared to be single except in a few cases.

The mesophyll is stimulated to excessive growth which causes a thickening of the leaf (A). The epidermal cells around the infected cells grow so as to almost but never completely cover them (C). The infected cell is embedded in the tissues of the host except at point of infection. The host cells form a definite sheath around the infected cell (C).

SYNCHYTRIUM CHILTONII Cook on *Stellaria media* (L.) Cyrill. (FIGS. 3, E, F and FIGS. 4, A–D).

This fungus attacks the very young growths, mostly while in the bud. The fungus rarely fills the host cell until near maturity. Multiple infections are numerous; six or more fungi are frequently found in the same host cell (3, F); in most cases these fungi are the same or very nearly the same age, but in some cases they appear to be of different ages, as indicated by their development. The fungus grows rapidly and is usually granular or foamy in appearance. Two nuclei are occasionally present in the same fungus (4, C). The wall around the fungus is usually thin and the writer was not able to determine the number of layers. The contents of the host cell is usually inconspicuous but the host cell nucleus may persist until the fungus is about one-half mature.

The host tissues around the infected cells grow rapidly and cause thickenings of the infected leaves (4, A). The cortex of infected stems becomes very much thickened (4, B). The infected cells develop into rather large globular or oblong sacs which are not

filled until the fungus approaches maturity (4, A). In the stems, these sacs are embedded in the thickened cortex (4, B) and are oblong and longer than those in the leaves (4, B, C). The opening

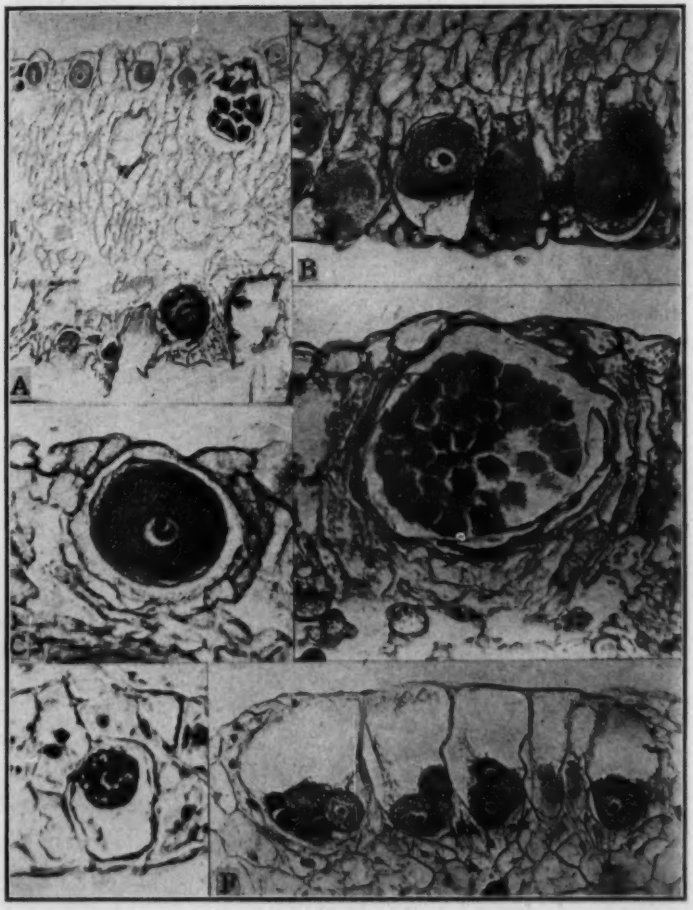

FIG. 3.

over the infected cell is never closed. A sheath of host cells is formed around the infected cell (4, A, C) and the epidermal cells at the opening are modified (4, A).

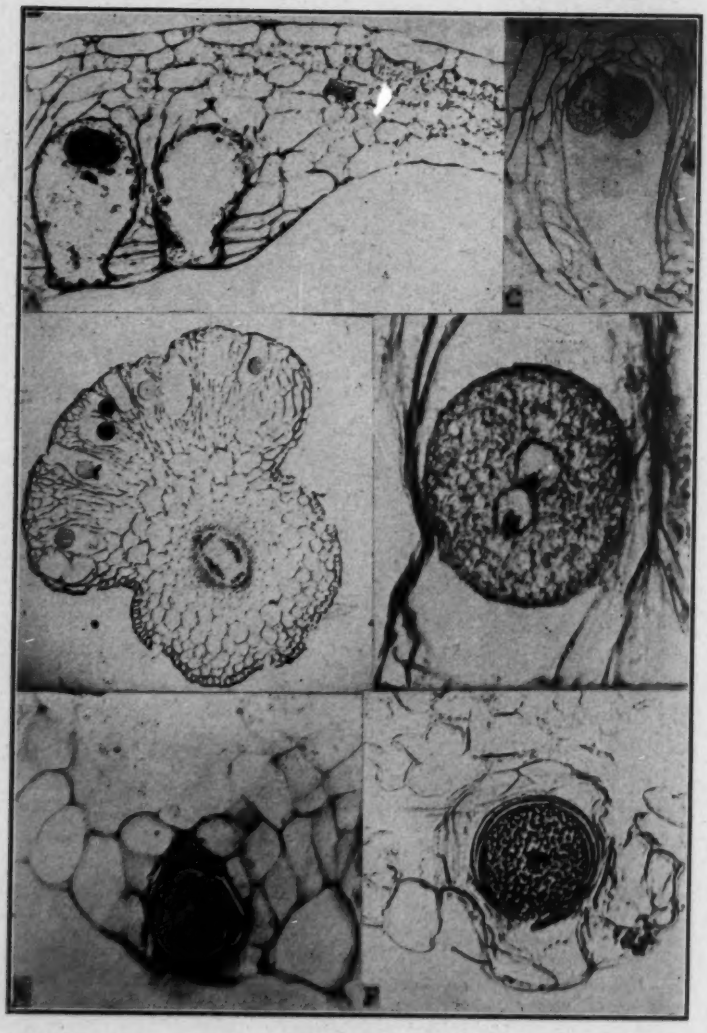

FIG. 4.

SYNCHYTRIUM CERASTII Cook on *Cerastium viscosum* L. (FIG. 4, E, F and FIG. 5, A–C).

The fungus grows so rapidly that a young, infected cell is soon filled (4, E, F) but in its later development the host cell grows more rapidly than the fungus and there is a large space between the fungus and the cell wall (5, A–C). Rarely one or more fungi are formed in a host cell but when two are present they are not necessarily the same age. The wall around the fungus is very thick when young (4, E, F) but becomes thin with age (5, A, C). It consists of three layers; the inner and middle layers are thin and usually so closely united as to appear as one. The disintegrating contents of the host cell are abundant at first, gradually decrease in amount (4, E, F). The host nucleus persists almost to time of segmentation of the fungus.

The galls are variable in size and, when abundant, they cause thickenings of the host tissues. The infected cell enlarges rapidly; the host tissues increase and almost surround it. When the infected cells are fully developed, they usually resemble the fully developed cells of *S. Chiltonii* (5, A) but are smaller and in some cases almost globular (5, B). The leaf thickens as a result of an increase in the amount of parenchyma and a sheath of one or two or three definite layers of cells is formed around the basal part of the infected host cell (5, A, B) which is embedded in the thickened host tissue. When the stems or petioles become thickened the infected cells are elongated and oval (5, C) and the surrounding cells very much modified to form sheaths around the infected cells.

SYNCHYTRIUM GERANII Clen. on *Geranium carolinianum* L. (FIG. 5, D–F and FIG. 6, A–C).

The fungus fills the infected cells soon after infection (5, D) but in a very short time these cells grow more rapidly than the fungus. The contents of the host cell is vacuolate at first but degenerates very rapidly. It is usually most abundant on the side next to the point of infection (5, F). It becomes granular as the fungus approaches maturity and is conspicuous (6, B). The host cell nucleus persists until very late, sometimes until the beginning of the segmentation of the fungus (6, A). The fungus appears to con-

sist of a foamy material (5, E) and contains an exceptionally large nucleus. It is surrounded by a wall consisting of three layers; the inner and middle layers are thicker than in most species and the inner is lighter in color; the outer layer consists of masses of dis-

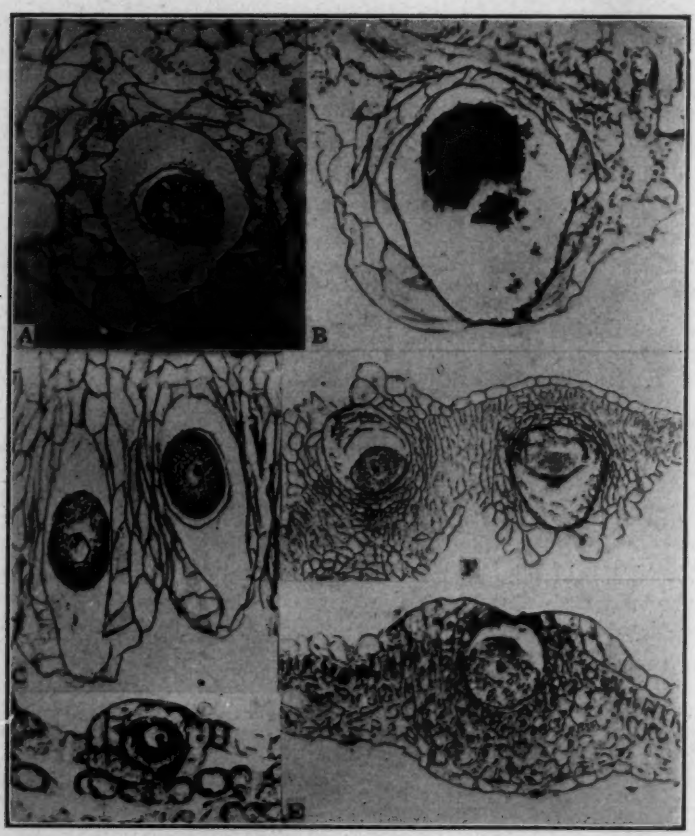

FIG. 5.

integrating contents of the host cell and is more conspicuous than in any other species reported in this paper (6, B). The inner and middle walls become very thin as the fungus approaches maturity (6, B).

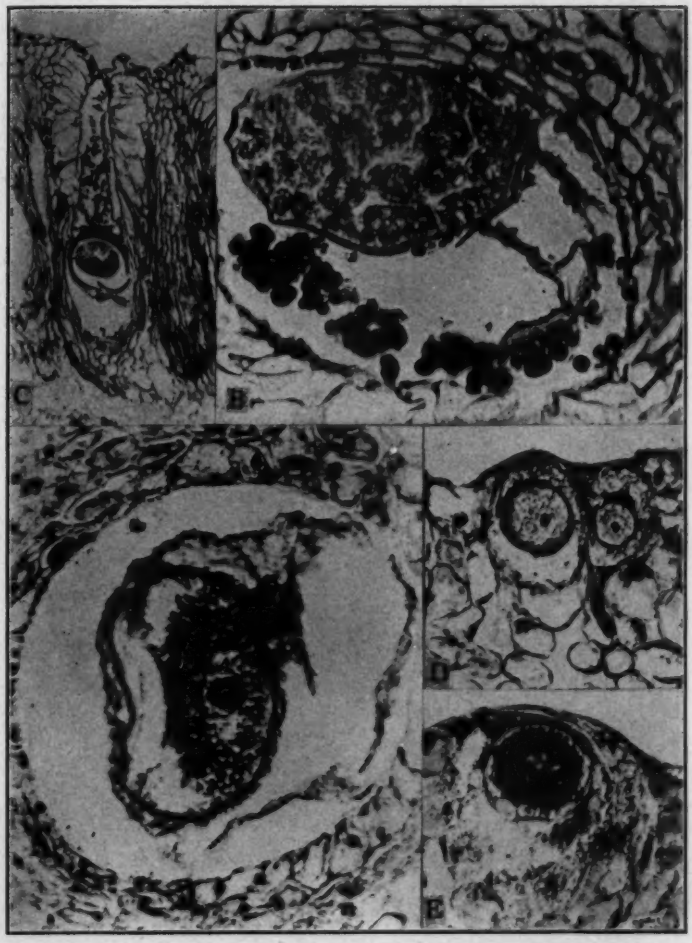

FIG. 6.

The galls caused by this species are conspicuous by their bright red color. They are both simple and compound and cause pronounced deformities of leaves, petioles, and stems. The stems are sometimes swollen and fleshy like small tubers. The infected cells grow rapidly and the surrounding host cells are stimulated to cause

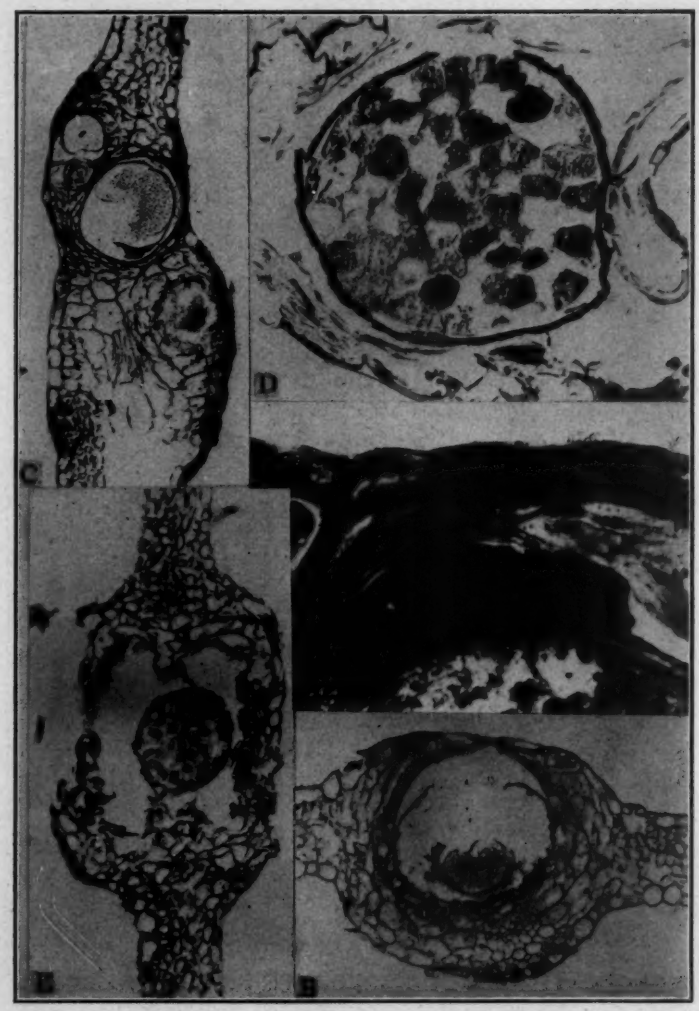

FIG. 7.

a thickening of the tissues. The basal half of the leaf gall is surrounded by a sheath of modified host cells and the lower half embedded in the host tissues. The outer half is conical with a definite opening in the center which extends to the infected cell (5, F).

The cells around this opening are large and prominent. The infected cells in the fleshy growths are very long, with the fungus in the basal part, and are surrounded by an abundance of disintegrating material especially in the outer part (6, C).

SYNCHYTRIUM EDGERTONII Cook on *Dichondra repens* Forst. (FIG. 6, D, E and FIG. 7, A–E).

The infections of various ages sometimes occur in the same leaf (7, C). The fungus grows more slowly than the infected cell at first and large quantities of disintegrating host cell contents are usually present (6, E) but the amount decreases later (7, D, E). After a time the fungus grows rapidly and sometimes fills or nearly fills the host cell (7, C). The fungus is surrounded by a very thick wall (7, D) of three layers; the inner and middle are very hard and frequently break when struck by the microtome knife. The outer layer, composed of disintegrate contents of the host cell, is abundant at first but decreases with age. In most cases this wall is very thin at maturity.

The infected cell grows rapidly (6, D, E) and stimulates the surrounding host tissues. The epidermal cells grow rapidly and close over the infected cell very quickly (6, E). The host cells grow over the infected cell so that it becomes completely embedded but the point of infection can be traced in the sections that are cut properly (7, A). In some cases the infected cell lies about equal distance between the epidermal layers while in other cases it is nearer one than the other. When the fungus approaches maturity the surrounding host cells are very large. In some cases the mature gall is visible on only one and in other cases on both surfaces of the leaves (7, C). Compound galls are of common occurrence (7, C). When the fungus is mature the surrounding host tissues die and the fungus falls out (7, E). The stem and petiole galls are in the cortex tissue which finally breaks down.

SYNCHYTRIUM LEPIDII Cook on *Lepidium virginicum* L. (FIG. 8, A–F).

Soon after infection the fungus grows rapidly and completely fills the host cell and then grows more slowly. The mature fungus

is larger than in most species. Multiple infections are common (A). The wall around the fungus consists of three layers (E); the inner one is very thin, the middle one slightly thicker, and the

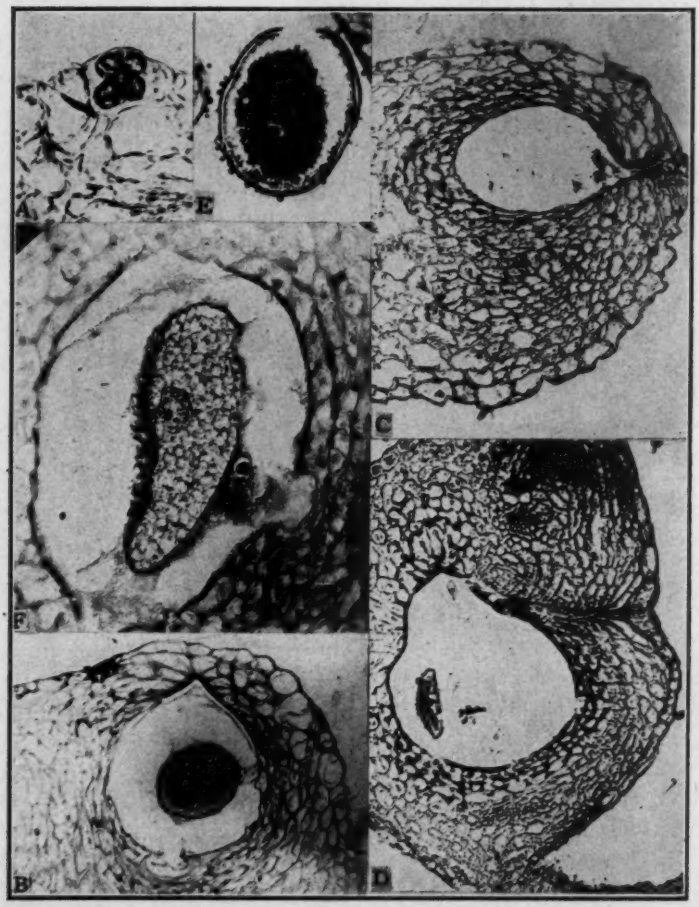

FIG. 8.

outer one almost non-existent although a few fragments of the disintegrating cytoplasm of the host cell may cling to the middle layer (E, F). In some cases it is almost impossible to distin-

guish between the inner and middle layers. In advanced stages the fungus does not fill the host cell (F).

The infected cells grow rapidly and the surrounding host cells are stimulated to excessive growths which cause galls that may be visible on either or both surfaces of the leaves and very conspicuous on petioles and stems. The growth around the point of infection is so great that the infected cell is completely embedded in the host tissues (B). The galls vary in form, are composed of a compact mesophyll of small cells; the cells next to the infected cells being the smallest (C, D). Compound galls are quite numerous. A very definite sheath is formed around the infected cell (B, D, F).

SYNCHYTRIUM AUREUM Schroeter on *Lactuca* sp. (FIG. 9, A–D).

This species attacks the epidermal cells on the lower surface of the leaves, rarely on the upper. The fungus grows rapidly and completely fills the host cell in its early development but in its later stages the infected host cell is slightly larger than the fungus (B, C). The wall around the fungus is thin and shows two distinct layers. The disintegrating contents of the infected cell is sparse. The nuclei of the infected cells are rarely seen.

The infections are almost entirely restricted to the lower surface of the leaf. The infection is followed by the formation of a dome-shaped structure with the concave side on the lower surface of the leaf (D). The galls are formed on the under surface regardless of whether the infection occurs in the lower or upper epidermis. In some cases the mesophyll cells just above the infected cell become elongated (A) while in other cases they are only slightly affected (B–D). However, the host tissues are modified more or less throughout the entire dome and in the palisade layer the cells are reduced to more or less cubical form.

SYNCHYTRIUM HYDROCOTYLES Cook on *Hydrocotyl umbellata* L. and *H. Canbyi* Coult. & Rose (FIG. 9, E, F and FIG. 10, A–C).

The fungus usually fills the infected cell until it is mature (10, A–C). Two fungi are occasionally observed in the same cell. The wall around the fungus is usually thin and it is difficult to de-

termine the number of layers. The disintegrating contents of the host cell is abundant but gradually decreases with age. The host cell nucleus is not prominent.

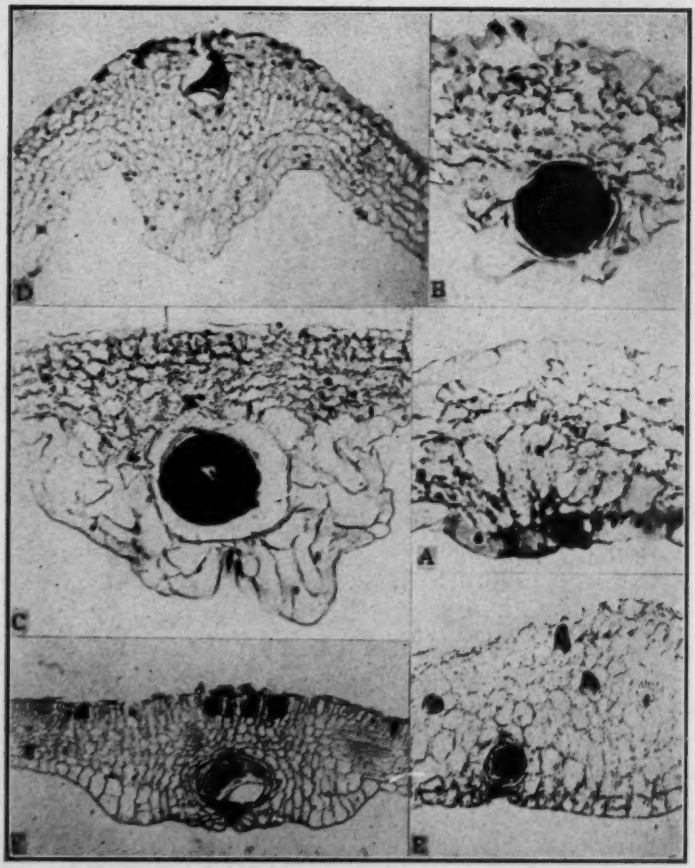

FIG. 9.

The infected cell grows rapidly and the surrounding tissues are stimulated to excessive growth and the formation of a dome with the concave side usually on the under surface of the leaf. However, when the infected cell is on the upper surface the concave

side is also on the upper side of the leaf. These concave structures are not formed on the margins of the leaves or petioles. The epidermal cells around the infected cell grow so that the opening is

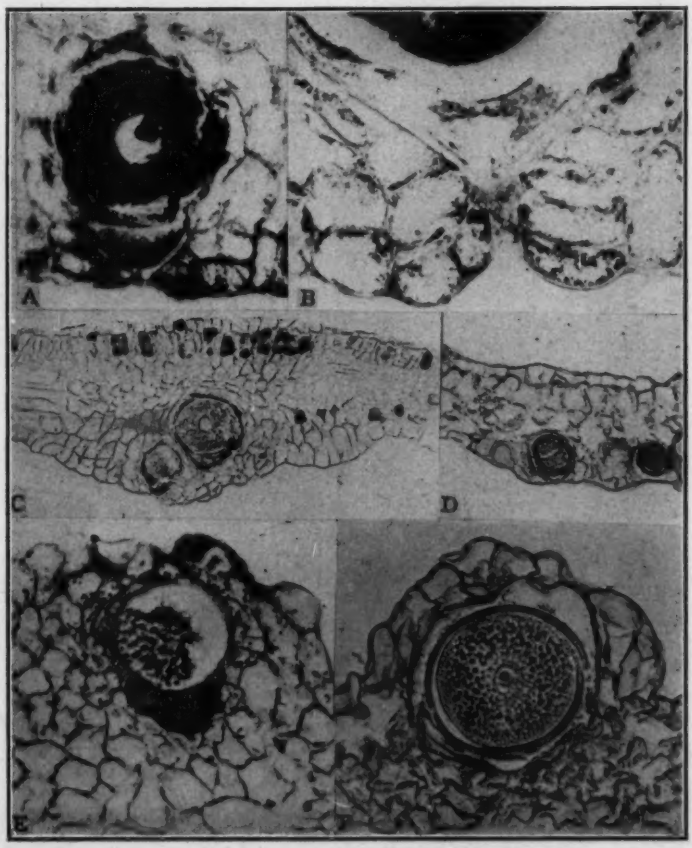

FIG. 10.

nearly or completely closed (10, B, C) but the openings can be traced if the sections are cut properly. Two fungi are sometimes found in the same gall, but one is usually older than the other. The mesophyll in the galls is composed of small compact cells.

SYNCHYTRIUM STACHYDIS Cook on *Stachys agraria* Cham. & Schlect. (FIG. 10, D–F and FIG. 11, A–C).

The fungus almost completely fills the infected cell and is about one-third full size before the start of gall formation. The wall around the fungus is thick until the fungus is about two-thirds full

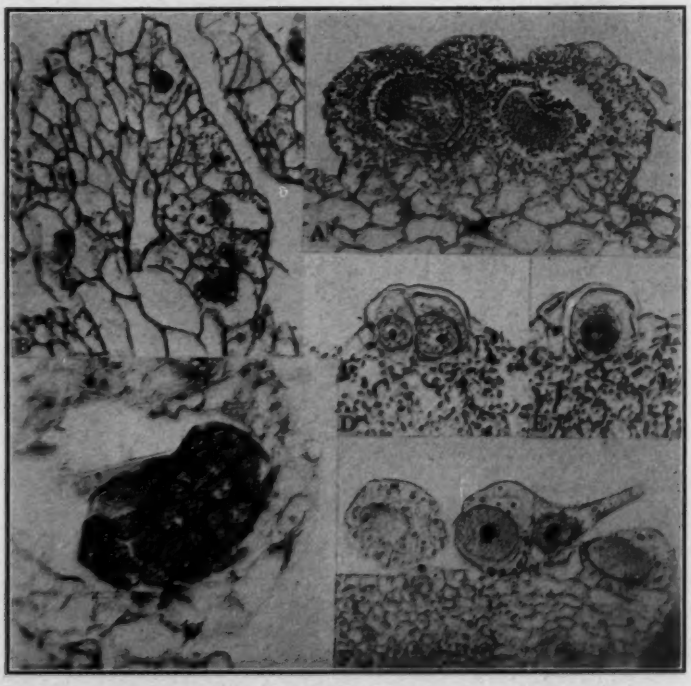

FIG. 11.

size (F). After that it becomes thin. It appears to be composed of three layers; the inner is thin, the middle thick (F) and the outer which is composed of degenerate contents of the host cell is abundant at first but decreases with age (E, F). The nucleus of the host cell persists until the fungus is about one-half full size.

Both the infected and the surrounding host cells grow rapidly. The epidermal and other host cells surrounding the infected cell

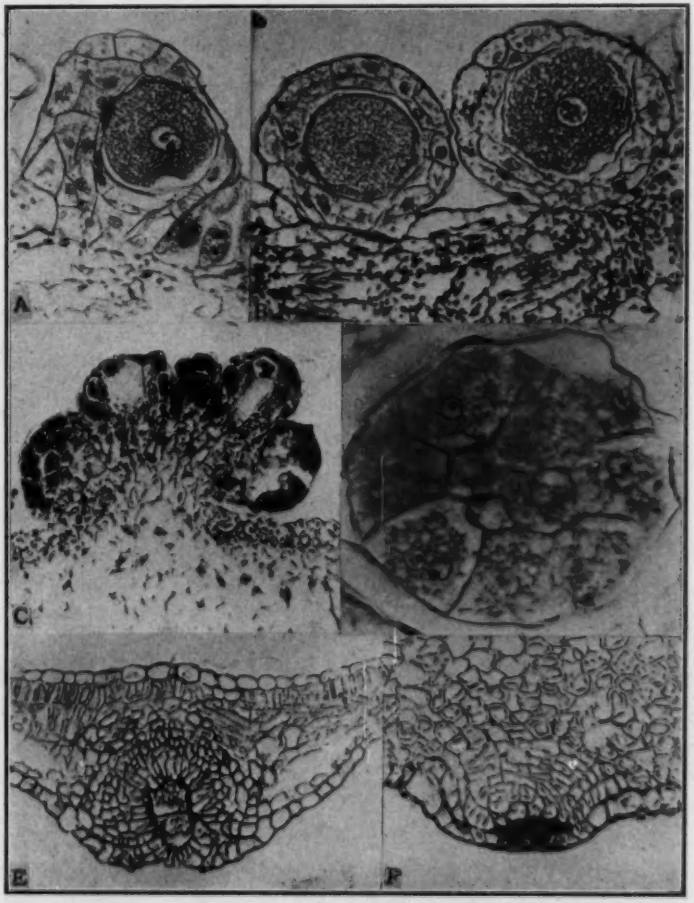

FIG. 12.

grow over and form a gall made up of large thin-walled cells with infected cell submerged at some distance from the surface. Many epidermal cells of this gall become infected and result in the formation of large compound galls (B).

The host plant is attacked by mites which cause galls that are frequently mixed with the galls caused by the *Synchytrium* but

can be distinguished in micropreparations by the different structures and frequently by the presence of the mites, especially in young mite galls.

SYNCHYTRIUM MODIOLIENSIS Cook on *Modiola caroliniana* (L.) G. Don. (FIG. 11, D–F and FIG. 12, A–D).

The fungus grows rapidly and fills or nearly fills the infected cell which also grows very rapidly (D, E). Two or three fungi in a single host cell is quite frequent. The only case of infection of a trichome was found in this species (F). The wall around the fungus consists of at least two very thin layers which are so closely united as to appear as one. The disintegrating contents of the infected cell is abundant and foamy in appearance at first but decreases very rapidly and practically disappears at maturity, so that there is little or no third layer in the wall around the fungus.

The galls are spherical unless crowded and rest on the surface of the host (A, B). There is very little modification of the host tissues. The epidermal cells on three sides of the infected cells grow so as to form a covering of about two layers, or sometimes three layers at the base, over the infected cell (A). The epidermal cells on the fourth side start to grow a little later and finally meet the growths from the other sides. The result is a small opening where the growths from the four sides come together that is a little to one side of the center (A). When a gall is cut properly this is very evident but when cut at right angles it is not visible (B). Galls on the stems may be irregular in form or undeveloped (C).

Imperfect galls.

In some cases the fungi die and the resulting galls are imperfect, the development depending on the period of infection before the death of the fungus (FIG. 12, E and F). This may occur in any species.

SUMMARY

The infections in the species reported in this paper always take place in epidermal cells of the host plant before they are fully mature and are more numerous on leaves than on other organs.

Some species appear to be able to attack epidermal cells that are more mature than other species.

In most cases the epidermal cells are infected by a single zoöspore but multiple infections have been found in every species and are quite common in some species, *S. Chiltonii* on *Stellaria media* and *S. Lepidii* on *Lepidium virginicum*, although less common on the latter. The fungi within the cells are usually of about the same age as indicated by development, but there are some exceptions, especially in the case of *S. Chiltonii*.

Both the infected host cells and the fungi continue to grow until the fungi are ready for segmentation. The fungus has a foamy appearance but finally becomes filled with spherical bodies which are probably oil globules. The nucleus is very large and clear, except for the presence of the nucleolus and dark staining materials.

The infections in a leaf area are usually very nearly the same age but there are some exceptions; *e.g., Synchytrium fulgens* on *Oenothera laciniata* and *Synchytrium Stachydis* on *Stachys agraria*.

The fungi enlarge until the host cells are practically filled. After that the infected cell in most species usually grows faster than the fungi.

All species studied cause the formation of galls but these abnormal structures caused by some species are much more conspicuous than those caused by other species (*e.g., Synchytrium Geranii*).

The epidermal cells immediately around the infected cell are excited to growth and in all cases except in that *S. fulgens* grow and divide in such manner as to form galls. The cells in contact with the infected cell are modified and form definite sheath structures around the infected cells. Some species cause very little or no modifications of host tissues (*e.g., S. modioliensis* and *S. Erigerontis*). Some species cause the infected leaves to thicken; the infected cells are embedded in these thickened leaves with very little or no gall formation. Some species cause the formation of galls on the surfaces of leaves and little or no modifications of the leaves (*e.g., S. modioliensis*).

The galls start with the growth of epidermal cells in contact with the infected cells but the cells of other tissues may be in-

volved later. In some cases one-half of the infected cell is submerged, while in other cases it may be completely submerged. This is due to the growth of the host tissues. In cases where the infected cell is completely submerged there may be no gall or only a thickening of the leaf (*e.g., S. Edgertonii, S. Erigerontis,* and *S. fulgens*).

The galls caused by different species of *Synchytrium,* for the most part, are distinctive and much more important for descriptions and determination than the characters of fungi that cause them.

Galls may be modified by overcrowding. Compound galls usually result from infections of epidermal cells of older galls.

The mature fungus of all species studied is embedded in the tissues of the host, except in the case of *S. modioliensis* in which the fungus exerts very little influence on the structure of the leaf. This gall rests on the surface of the leaf or other organ.

The infections on the petioles and stems cause growths of the cortex which usually result in malformations which are very pronounced in some species.

In some species there is a definite opening to the infected cell until maturity of the fungus, while in other species the infected cell is completely enclosed in the gall which is formed from the surrounding host cells. However, a definite line between the host cells that have closed over the infected cells can be traced if the sections are cut properly.

The author wishes to express his thanks to Dr. C. W. Edgerton and others who have assisted in and given encouragement to this work. They have been mentioned in the preceding paper. Dr. Edgerton made all the photographs.

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EXPLANATION OF FIGURES

FIG. 1. A–D, *Synchytrium Erigerontis* Cook. A, Early infections in lower epidermis (× 224). B, Advanced stage, not exactly through the center; note wall around fungus and small amount of disintegrating contents of host cell (× 392). C, Infection in upper surface of leaf; note that the infected cell extends from epidermis to epidermis, and that it is not completely

covered by the upper epidermis (× 192). D, Two hemispherical fungi in a single host cell (× 192). E, F, *S. globosum* Schroeter; E, Gall and infected cell; note large cells of gall and disintegrating contents of infected cell (× 192). F, Same showing many small sporangia (× 192).

FIG. 2. A–E, *S. Lythri* Cook. A, Showing thickened leaf of host plant and early infections; the infected cells near the upper surface that appear to be submerged have not been cut through the center (× 96). B, Early infection in a stem. C, Shape of infected leaf cell surrounded by sheath formed from host cell tissue (× 224). D, A much later stage with lower magnification; note long tube and modified cells at surface (× 144). E, Showing fungus with thin wall and disintegrating host cell nucleus (× 384).

FIG. 3. A–D, *S. fulgens* Schroeter. A, Showing thickened leaf of host and infections of different ages on both surfaces of leaf (× 192). B, Showing early infections on lower surface of leaf. C, Showing growth of epidermal cells, partially covering infected cell and sheath of host cell tissue around infected cell (× 192). D, Showing large number of small sporangia and that the epidermal cells have not completely covered the infected cell (× 192). E–F, *S. Chiltonii* Cook. E, Showing a single infected cell on lower surface of leaf (× 312). F, Showing single and multiple infected cells on upper surface of leaf (× 192).

FIG. 4. A–D, *S. Chiltonii* Cook. A, Showing two large infected cells in lower surface of leaf surrounded by modified host cells; part of leaf to the right is not modified (× 66). B, Showing thickened cortex on one side of stem (× 16). C, Showing infected cell of infected stem with two fungi and modified host tissue (× 80). D, Showing a large fungus with two nuclei (× 280). E, F, *S. Cerastii* Cook. E, Showing early infection on under surface of leaf (× 328). F, Showing a later stage (× 280).

FIG. 5. A–C, *S. Cerastii*. A, Showing the shape of the infected cell in advanced stage and the sheath of host tissue around it (× 134). B, Showing slightly different form of infected cell and sheath of host tissue (× 160). C, Showing infected cells with surrounding sheath of host tissue in stems (× 140). D–F, *S. Geranii* Clen. D, Showing early infection in lower surface of leaf (× 280). E, Showing early development of gall in upper surface of leaf and that the epidermal cells have not closed over the infected cell (× 160). F, Showing advanced development of galls on both surfaces of leaf; note sheath of host tissue around infected cells, that the infected cells are not covered by the epidermal cells and the large epidermal cells around the opening (× 66).

FIG. 6. A–C, *S. Geranii*. A, Showing fungus and host cell nucleus (× 312). B, Showing stage in formation of sporangia and disintegrating content of host cell (× 312). C, Showing a single infected cell from fleshy stem; note shape, sheath of host tissue and disintegrating contents of host cell (× 50). D & E, *S. Edgertonii* Cook. D, Showing two infected cells in upper epidermis of leaf (× 312). E, Showing more advanced infection in upper epidermis of leaf and growth of epidermal cells over infected cells and disintegrating contents of host cells (× 312).

FIG. 7. A–E, *S. Edgertonii* Cook. A, Showing the complete closing of the host cells over the infected cell but that the line of union can be traced (× 624). B, Showing a gall that originated from a cell in upper epidermis

and the modified host cells around the infected cell (×96). C, Showing compound gall and infections of different ages (×66). D, Showing an advanced stage in development of sporangia (×312). E, A mature gall in which the host tissues are disintegrating (×96).

FIG. 8. A–E, *S. Lepidii* Cook. A, Showing early multiple infection on lower surface of leaf (×280). B, Advanced stage showing young gall and the closing of the host tissues over the infected cell (×80). C & D, Showing two galls composed of compact, small mesophyll cells and the opening to the infected cells (×80 and ×66). E, Showing fungus with two nuclei, the wall around the fungus and the small amount of disintegrating contents of the host cell (×280). F, Showing a fungus and nucleus of the host cell; note the notch in the surrounding host cell tissue (×200).

FIG. 9. A–D, *S. aureum* Schroeter. A, Showing early infection in cell of lower epidermis and modifying host cells of the mesophyll (×160). B, More advanced stage in which the mesophyll is not modified but surrounding epidermal cells are enlarged (×160). C, More advanced stage showing the enlarged cells of the gall (×134). D, Showing infection in the upper epidermis and an advanced stage in the formation of the gall on the under surface; also showing the dome over the gall (×80). E & F, *S. Hydrocotyles* Cook. E, Showing an early infection on the under surface of the thickened leaf (×66). F, A later stage showing the closing of the host tissues over the infected cell and the disintegrating contents of the infected host cell (×66).

FIG. 10. A–C, *S. Hydrocotyles* Cook. A, Later stage showing growth of infected cells over infected cell (×280). B, Showing closing of the host cell tissues over the fungus at point of infection (×280). C, Showing two fungi of different ages in the same gall (×66). D–F, *S. Stachydis* Cook. D, Showing infection of leaf (×120). E & F, Showing later infections, wall around the fungi and degenerate contents of host cell (×328).

FIG. 11. A–C, *S. Stachydis* Cook. A, Showing two galls in early stages of development (×160). B, Showing infections in epidermal cells and also one cell with three sori. C, Showing sporangia (×328). D–F, *S. modioliensis* Cook. D, Showing early infection of two epidermal cells in upper epidermis (×312). E, Showing an infected cell and first growth of an epidermal cell (×312). F, Showing infection of an epidermal cell (×160).

FIG. 12. A–D, *S. modioliensis* Cook. A, Showing almost complete gall in which the epidermal cells are meeting to one side of center (×280). B, Showing two galls; the one on the right shows the opening to the infected cell; the one on the left is cut at right angles to the first and the opening is not shown (×280). C, Showing crowded galls on stem (×160). D, Showing sporangia (×66). E, *S. Geranii*, showing imperfect gall following death of fungus (×80). F, *S. Lepidii*, showing imperfect gall following death of fungus (×160).

A COMPARATIVE STUDY OF TWO CLOSELY RELATED ROOT-ROT FUNGI, CLITOCYBE TABESCENS AND ARMILLARIA MELLEA

ARTHUR S. RHOADS [1]

(WITH 5 FIGURES)

INTRODUCTION

The root rots produced by these two closely related mushroom or toadstool fungi are so much alike in general aspect that, in the absence of sporophores or the isolation of the fungus, they may be confused readily. The correctness of the diagnosis of these root rots made under such circumstances, particularly in sections where both possibly occur, may be questionable in some cases.

Considerable confusion also has existed for many years in the literature with respect to the identity of *C. tabescens* Scop. ex Bres., despite Bresadola (**3**) having shown in 1900 that the united *Clitocybe* best known in the United States as *C. monadelpha* (Morg.) Sacc. is identical with the European plant described as *Agaricus tabescens* by Scopoli in 1772. Even more than two decades after the publication of Bresadola's work, with many mycologists accepting the identity of the fungus in its true light, we find Rea (**10**), Buller (**5**, p. 91), and certain others regarding it merely as an exannulate form of *A. mellea* Vahl ex Fr. The writer in 1925 (**12**) published the taxonomy of *C. tabescens*.

The following, subsequently published remarks by Kauffman (**7**, pp. 206–207), who accepted Bresadola's consideration of the American plant in question as synonymous with *C. tabescens* of Europe, are of interest in this connection:

[1] Formerly Plant Pathologist of the Florida Agricultural Experiment Station, in charge of the Citrus Field Laboratory at Cocoa, where the work here reported was done. Acknowledgment is made to the Division of Forest Pathology of the U. S. Department of Agriculture for their interest and support, which have made it possible to prepare the results for publication.

"Under this name Morgan's American species, *C. monadelpha*, has finally come to rest—let us hope—in peace. There are still amateurish workers, who get a reaction out of suspecting that *C. tabescens* may after all be only a form of *Armillaria mellea*, and perchance a few who try to blow the breath of life into the long buried corpse of *Clitocybe parasitica* Wilcox, in order to show that it was either *C. tabescens* or *Armillaria mellea* or a genuine species." Under the heading of "Synonymous and excluded or doubtful species" he remarked: "*C. parasitica* Wilcox was never understood by mycologists, and should be deleted from the literature."

How delightfully simplified mycology could be rendered by the simple expedient of relegating to a state of innocuous desuetude those species that are not understood. It is obvious from a consideration of Wilcox's description and illustrations (**20**) that there can be no question in regard to the identity of the Oklahoma root-rot fungus which he described as *C. parasitica*. But it was unfortunate that he considered it a distinct species from the one that had been so well described from Ohio by Morgan (**9**) as *Agaricus* (*Clitocybe*) *monadelphus*, basing his distinction simply on slight differences in morphology and the parasitic habit of growth. As the writer (**12**) has pointed out previously, Wilcox's assertion that the Oklahoma fungus "is always parasitic in habit" is contradicted subsequently by his own statements, and the slight morphological differences claimed by him are of little value. American mycologists, with the exception of Kauffman, appear to have been in general agreement that the species described by Wilcox is synonymous with Morgan's *Agaricus monadelphus*. It has long been recognized that this fungus occurs both parasitically and saprophytically, not only in Oklahoma but also in the adjoining States of Arkansas and Missouri and a number of others, chiefly southern ones.

Another point in Wilcox's paper (**20**) subject to criticism is his mention and illustration of black, stringlike, rhizomorphic strands, both cortical and subterranean, similar to those commonly associated with *A. mellea*, as a characteristic feature of the *Clitocybe* root-rot fungus in Oklahoma. Despite extensive field studies of the disease caused by this fungus in Florida over a period of 18 years, the writer has never observed the occurrence of such struc-

tures in connection with it,[2] though they have been observed in connection with the root rot caused by the closely related fungus, *A. mellea*. Wilcox (**20**) stated that subterranean rhizomorphs grew out into the soil for considerable distances from attacked trees, citing 8 feet in one case and 10 feet in another. Although he stated that, so far as he was aware, *A. mellea* did not occur in Oklahoma, a careful study of his bulletin, together with the fact that both this fungus and *C. tabescens* have been reported (**1**, p. 48) as "commonly parasitizing a number of plants, including privet hedges, apple and peach trees, as well as grape vines" in Arkansas, has forced the writer to conclude long ago that both fungi occur in Oklahoma and that the similar root rots caused by them must have been confused by Wilcox in the absence of cultural studies. This conjecture is further supported by the fact that Wilcox (**20**, p. 19) mentioned that he had detected the phenomenon of phosphorescence in the subterranean rhizomorphic strands. A recently published host index to plant diseases in Oklahoma (**4**) lists both root-rot diseases. *A. mellea* is listed as occurring on apple, blackberry, cherry, elm, maple, plum, privet, rose and sycamore, while *C. tabescens* is listed as occurring on apple, cherry, grape, peach and plum.

The close relationship between *C. tabescens* and *A. mellea* as observed by Totten (**19**) and Richards (**18**) in preliminary cultural studies, as well as in the investigations of the writer (**12**) in Missouri, and subsequently in Florida (**13**) over a period several years, have prompted him to make a comparative study of these fungi. While it was necessary to abandon this work before it was carried to the point desired, the results thus far secured have revealed striking and consistent differences that should definitely refute the view expressed by a number of mycological workers that *C. tabescens* is merely a form of *A. mellea*.

SOME DISTINGUISHING CHARACTERS OF THE ROOT ROTS

Despite the great similarity of *C. tabescens* and *A. mellea* with respect to their mode of attack and the symptoms exhibited by attacked plants, their ability to develop either parasitically or sapro-

[2] The rhizomorph indicated by him on the grapevine rootstock in Missouri (**12**, pl. 2) is now considered questionable.

phytically, and their marked predilection for oak roots, there are a number of features in which these root rots, as well as the fungi producing them, differ.

While both fungi commonly develop whitish- or chamois-colored rhizomorphic strands and sheets between the bark and the wood of attacked roots of woody plants, and also in pure cultures, according

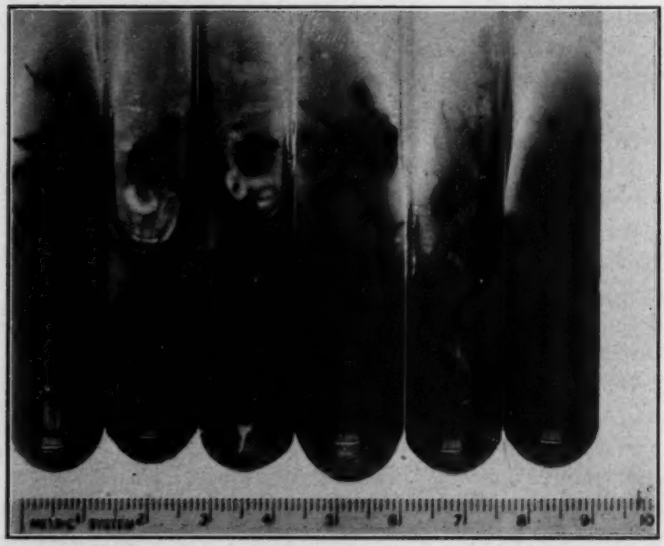

FIG. 1. Cultures of *C. tabescens* 10 days after inoculation with isolate from poinsettia, showing extensive development of rhizomorphs in comparison with scant growth of mycelium.

to the writer's observations the black, rounded or flattened, cortical and hypogeal, stringlike rhizomorphs so commonly produced by *A. mellea* are not produced by *C. tabescens*. But, both fungi may develop blackish, indurated, xylostroma outgrowths extruded through longitudinal fissures in the bark of attacked roots.

The peculiar perforate character of the mycelial sheets of *C. tabescens* pointed out by the writer (**16**) and described in detail (**17**), though not always well developed, is a characteristic feature of the root rot caused by that fungus, but appears to be lacking in

the case of the root rot caused by *A. mellea*. Moreover, the mycelial sheets in the case of *C. tabescens* appear to have a less pronounced fan-shaped type of marginal development than in *A. mellea*. Further differences between these closely related root-rot fungi in pure cultures are pointed out in the following section.

COMPARATIVE GROWTH AND FRUITING OF THE FUNGI IN PURE CULTURES

A few investigators have grown *C. tabescens* in pure cultures and, where cultures of *A. mellea* were available, the close resemblance of these two fungi has prompted comparisons. The basis for these comparisons heretofore has been limited to a few isolates. In 1917, Totten (**19**) reported growing both fungi in pure cultures on several media and showed that, while closely related, they are distinct. In 1921, Siggers [3] prepared a progress report of his comparison of *C. tabescens* isolated from a specimen of eucalyptus root sent from Florida and *A. mellea* isolated from a rhizomorph attached to the root of a white ash at Madison, Wis. In 1923, Richards (**18**), who continued this work after Siggers left for Central America, briefly reported on cultural studies of these fungi, comparing the isolate of *C. tabescens* from Florida with 6 isolates of *A. mellea* from various sources. The close similarity in appearance of cultures of these fungi was pointed out, and slight differences in *A. mellea* from different hosts were shown. She reported that *C. tabescens* produced sporophores but that all efforts to obtain them from *A. mellea* failed. In 1925, the writer (**12**) reported the results of cultural studies of *C. tabescens*, comparing his isolate of this fungus from grapevine in Missouri with the isolate from eucalyptus from Florida, which grew with greater luxuriance.

During the course of his investigations in Florida the writer has studied isolates of *C. tabescens* from a great array of host plants from this State and a number from trees in other States, including 5 from Alabama, 2 from Louisiana and 1 each from the District of Columbia and Virginia. The isolates of *A. mellea* that have been studied comprise 4 from Canada, 3 from California, 1 from Wisconsin, 2 from Pennsylvania, 2 from Florida, and 6 from Euro-

[3] Siggers, Paul V. Summary of comparative study between forms of *Armillaria mellea* and *Clitocybe monadelpha*. Typewritten report. 1921.

pean and other countries, the latter consisting of isolations by Cool, Gregor-Wilson, Rant, Reitsma (2), and the Centraal-Bureau voor Schimmelcultures. In addition, the tropical analogue of this fungus, *A. fuscipes* Patch, was represented by isolates from *Albizzia*

FIG. 2. Bottom of flask culture of *C. tabescens* from horsetail beefwood (*Casuarina equsetifolia* L.), showing radiating wrinkles in broad, thalluslike rhizomorphs and average growth of 2.5 cm. in 24 hour period following outlining of margins. Natural size.

lophantha Benth. and *Camellia sinensis* (L.) Kuntze made by Gadd.

The rapidity of mycelial growth and rhizomorph formation in *C. tabescens* have shown considerable variation in the different isolates, being fairly rapid in some and quite slow in others. Some

isolates of the fungus have developed a luxuriant growth of rhizomorphs starting within 3 days to a week. In many cases the development of rhizomorphs started and made considerable headway before there was any appreciable growth of mycelium on the surface of the agar. In other cases, however, the development of the rhizomorphs was less rapid and occurred only after the development of more or less mycelial growth on the surface of the agar. In some cases little or no development of rhizomorphs occurred. These differences were not necessarily confined to certain isolates of the fungus from particular plants. Even in a series of isolations from a particular plant or a series of transfers from a single isolate considerable variation occurred, with the result that some cultures grew rapidly and made a luxuriant development of rhizomorphs, while others grew slowly, with very scanty development of rhizomorphs. Transfers from old cultures in which the mycelial mat on the surface of the agar slant had developed a hard, brittle crust did not develop with the readiness of transfers from younger cultures. In some instances subcultures from cultures that developed rhizomorphs luxuriantly developed few or none. In most cases, however, it was found that rhizomorph development could be greatly stimulated by transfer to a rich nutrient medium.

A. mellea behaved similarly and proved even slower and more temperamental in culture. Reitsma (**11**) found that the formation of rhizomorphs by this fungus was completely suppressed by constant subculturing in liquid media but that upon transference to a solid substratum rhizomorphs gradually developed again. Lisi (**8**), who studied 47 isolates of this fungus from a wide variety of habitats and localities, found many distinct varieties, a number of isolates studied from a restricted geographical area showing at least 6 distinct variants. He made a physiological study of a selected group of 10 morphologically distinct variants. Benton and Ehrlich (**2**) found a wide variation in the character of mycelial growth, rhizomorph production, and rate of growth in 10 isolates of *A. mellea* from a single suscept species (*Pinus monticola* Lamb.), though the replications from a single isolate were found to have similar cultural characteristics. They also found the tested isolates to vary in degree of saprogenicity and in response to differences in wood-moisture content, temperature, and pH values.

The writer has found that the nutrient medium exerts considerable influence on the character, rate, and luxuriance of growth of the mycelium and rhizomorphs in both *C. tabescens* and *A. mellea*. Cultures of these fungi on potato-dextrose agar usually developed slowly and tended to make a rather weak growth. The addition of maltose or malt extract or other sources of sugar greatly stimulated mycelial growth and rhizomorph production. It was found in the writer's earlier cultural work in Missouri (12) that *C. tabescens* grew well on prune and raisin agars. Most of his cultural work in Florida with both this fungus and *A. mellea* has been conducted on the standard potato-dextrose agar with the addition of 20 gms. of either maltose or malt extract per liter. In some cases a little cane sugar was added. The addition of peptone to such agar was not observed to stimulate greater luxuriance of growth. For flask cultures such plant material as oak sawdust, diced potatoes, carrots or bread, pieces of petioles of castor bean leaves, or cubes of oak wood or banana stems have been added to the agar. The addition of oak sawdust appeared to induce a more vigorous, whiter, and fluffier growth of mycelium. On the latter medium *C. tabescens* made a much more rapid growth than *A. mellea*, which Edgecombe (6) found to be an exceedingly slow grower on artificial media in comparison with 5 other wood-inhabiting fungi.

Both fungi are characterized by the common, but by no means invariable, tendency for the agar to develop a dark brown discoloration in advance of the mycelial growth. In isolations of these fungi from roots and in transfers of them from stock cultures a distinct browning of the agar in advance of the inoculum frequently developed before mycelial growth became visible to the unaided eye. This browning of the agar appeared to develop principally in the cases where the cultures ran chiefly to mycelium rather than to rhizomorphs. The discoloration of the agar increased with the growth of the fungi until in cultures a month old the upper half of the agar slant in test tubes may become discolored dark brown.

RHIZOMORPH PRODUCTION

The characteristic feature of both *C. tabescens* and *A. mellea* is the usual early development of whitish rhizomorphs growing downward into the agar from the inoculum. Even in cultures of *C.*

tabescens started from basidiospores, rhizomorphs invariably develop before there is much growth of mycelium. In fact both fungi frequently run more to the production of rhizomorphs than of mycelium, though the development of rhizomorphs varied according to the culture media and the vigor of the isolate.

In transfers of bits of mycelium from either roots or cultures a series of whitish rhizomorphs usually developed from the bottom of the inoculum simultaneously with or shortly after the beginning of mycelial growth on the surface of the agar in the case of both fungi. These rhizomorphs grow downward into the agar fairly rapidly as rounded or flattened, simple or branching, tortuous, antlerlike structures, the tips of which may be pointed, blunt, or flattened (FIG. 1). As these rhizomorphs became older numerous, short, threadlike, lateral branches often developed. In vigorously growing cultures the rhizomorphs commonly ramified through the agar in all directions. Occasionally one or more of them became greatly flattened and thalluslike in appearance, though this type of rhizomorph rarely developed in test tube cultures.

After growing down into the agar in test tube and flask cultures the ends of some of the rhizomorphs soon turned upwards of their own volition and developed until their tips pushed through the surface of the agar, after which there was little further elongation. In *C. tabescens* the tips remained characteristically blunt and rarely protruded more than $\frac{1}{16}$ to $\frac{3}{32}$ of an inch above the surface of the agar and remained light-colored, though darkening somewhat with age. In *A. mellea*, however, the tips often projected as much as $\frac{1}{4}$, and occasionally $\frac{1}{2}$, inch, turning dark reddish-brown to blackish following exposure to the air and became attenuated or needlelike. The development of these elongated, dark reddish-brown to blackish, needlelike, aerial rhizomorphs protruding above the surface of the agar varied somewhat in cultures from different sources and was most pronounced in *A. fuscipes*. The dissimilar character of the aerial rhizomorphs is one of the main distinguishing characters between *C. tabescens* and *A. mellea*, including its tropical analogue. Up to the point where the rhizomorphs protrude through the surface of the agar these two fungi appear to be inseparable on the basis of rhizomorph development since either may exhibit a considerable range of variation. The rhizomorphs

that develop down into the agar remain white for a time in both fungi but become chamois-colored with age.

The growth and development of the rhizomorphs are best studied in flask cultures, where they may be observed growing along the bottoms and up the sides. In both *C. tabescens* and *A. mellea* all

FIG. 3. A, Second production of sporophores in 6 week old cultures of *C. tabescens* from poinsettia, the tubes from left to right first developing mature ones in 28, 33 and 38 days, respectively. B, cluster of mushrooms developed from end of rhizomorph at top of agar slant in 18 mm. test tube 31 days after isolation from painted copperleaf.

gradations of rhizomorph formation from simple or branching, threadlike ones to much-branched, greatly broadened, thalluslike structures as much as an inch wide at the ends (FIG. 2) may be found in an assortment of cultures from different isolates. The latter type of rhizomorphs, which occurred much more frequently than the former, is characterized by a series of radiating wrinkles.

After the fungi became well established the rhizomorphs often developed for a time with considerable rapidity. In order to secure some accurate measure of the rate of growth attained under favorable conditions, the marginal outlines of a number of broad, thalluslike rhizomorphs growing across the bottom of a 500 ml. Erlenmeyer flask culture of *C. tabescens* at a laboratory temperature of 24° C. were outlined at noon of one day with a pen, using photographer's opaque. By noon of the following day, when the flask was photographed (FIG. 2), the rhizomorphs had finished growing across the bottom of the flask and turned up along one side, making an average advance of 2.5 cm. during the 24-hour period. In a similar flask culture of *A. mellea* growing under the same conditions thalluslike rhizomorphs ranging from ½ to 1 inch wide grew in length from 1 to 1.5 cm. during the same period. Both were growing on potato-dextrose-maltose agar with sawdust and cubes of oak wood. As a general rule, *C. tabescens* grew much more rapidly than *A. mellea* under the same conditions in all cases where comparisons were made.

MYCELIAL GROWTH

The growth of the surface mycelium in both fungi was quite variable in regard to rate, character, and color, even in a series of isolations from one plant or a series of subcultures from a given isolate. It usually developed very slowly regardless of whether rhizomorphs formed or not and frequently no appreciable growth of mycelium developed until after a fairly extensive development of rhizomorphs. In most cases mycelial growth was fairly luxuriant after it developed but in other cases the growth was very meager and test tube cultures frequently dried up before the surface of the agar slant became covered.

The initial growth from the inoculum in *C. tabescens* started as a white, velvety mycelium but subsequent growth was closely appressed to the surface of the agar, forming a compact mat. The color changes varied considerably according to the luxuriance of growth and age of the culture. The white mycelium first formed soon turned tawny and then pale tan to light brown in the majority of moderately young cultures. As the cultures became older the mycelium gradually darkened and the older parts usu-

ally became cinnamon-brown to dark reddish-brown or sepia-colored. In actively growing cultures the marginal growth frequently remained white while the older portion of the mycelial mat became progressively darker toward the center, sometimes with a slight zonate effect. In slow-growing cultures or old ones, however, there was a less striking contrast of colors and the white marginal growth may darken similarly to the color of the older portion. The older part of the mycelial mat became thickened irregularly and sometimes with a floccose, nodular, or tufted effect. The margin of the mycelial mat usually terminated abruptly but tended to become effused in slow-growing cultures. Sometimes, especially in very slow-growing cultures, simply a thin, pulverulent growth developed over the surface of the agar. Minute drops of brownish liquid frequently exuded from the mycelial mat.

In both fungi, shortly after the tips of the rhizomorphs protruded through the surface of the agar a white, appressed mycelial growth began to spread from them. This mycelial growth gradually became denser and thicker and later darkened to match the color of the older portion of the mycelial mat that developed from the point of inoculation. In this way, particularly in flask cultures of these fungi, new areas of mycelial growth may develop at several points on the surface of the agar in advance of the slow-growing mycelium developing from the point of inoculation, later coalescing with it. In both fungi also, when the rhizomorphs at the bottoms of test tubes became exposed by shrinkage of the agar away from the walls, they developed a white, downy growth of mycelium (FIG. 3, A).

In *A. mellea* the growth of the surface mycellium was similar to that of *C. tabescens* in most respects but differed in others. The initial growth from the inoculum was a white, velvety mycelium but subsequent growth as a rule was less compact and more wooly than in *C. tabescens* and soon became light tan, which was the prevailing color in the majority of cultures. With age, however, the mycelium usually became reddish-brown to sepia-colored. Moderately young cultures of the two fungi so closely resemble one another that they did not appear distinguishable as a rule on the basis of the color of the surface mycelium but *A. mellea* was

characterized by a more tufted and more floccose type of growth and this afforded the most striking visual means of distinction. With age, the mycelial mat also became thickened and so tough that it was difficult to make transfers without tearing up the cultures.

In test tube cultures of *C. tabescens* from 2 to 4 weeks old the rhizomorphs occasionally developed a halo-effect which, when examined with a hand lens by transmitted light, was seen to be due to a dense but delicate growth of hyphae radiating at right angles from the rhizomorphs. This halo-effect began just back of the growing tips of the rhizomorphs and gradually became broader with increased distance from the ends, until attaining a length of about 5 mm., measured radially from the rhizomorph. The effect

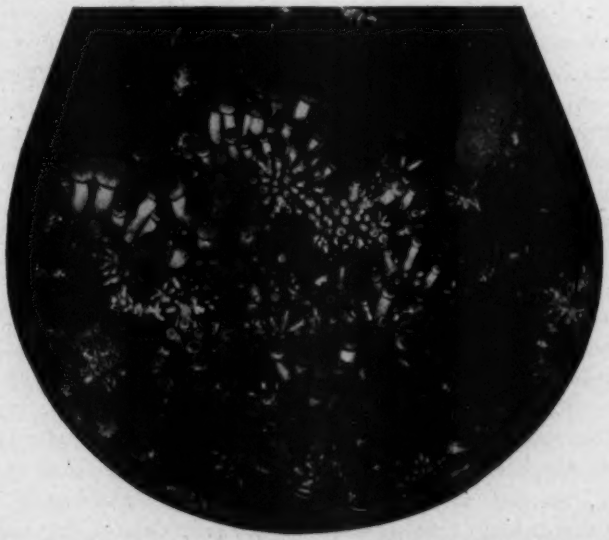

FIG. 4. Large number of buttons of *C. tabescens* developed in 500 cc. flask 3⅜ months after inoculating with isolation from sweet acacia (*Acacia farnesiana* Willd.).

is similar to the root-hair development on a radish seedling except that the radiating hyphae were much more minute and dense in comparison. In cultures of *C. tabescens* where only a series of

numerous, short rhizomorphs developed, a dense growth of hyphae has been observed occupying the upper portions of tube cultures, giving them a distinctly cloudy effect, especially when examined by transmitted light. A similar development of hyphae radiating from the rhizomorphs has been observed occasionally in test tube cultures of *A. mellea.*

In transferring cultures of both fungi to flasks it was noted repeatedly that where the inoculum was moved around the surface of the agar in placing it, growth of the fungi frequently developed simultaneously from numerous points. This suggests the possibility of secondary spore formation.

LUMINESCENCE

It has long been known that the mycelium of *A. mellea* is characterized by exhibiting the phenomenon of luminescence or noctilucence. It has been established that the luminescence of the mycelium is influenced by external conditions as well as by its age and conditions of growth. The addition of certain chemicals has been shown to increase luminescence, while others, such as anesthetics which interfere with protoplasmic activity, may reduce or entirely inhibit the capacity for luminescence. Reitsma (11) found that the percentage of cultures showing luminescence varied on different media and that on cherry agar it was limited to the points of the aerial rhizomorphs. Lisi (8) reported that 9 of a selected group of 10 morphologically distinct variants of *A. mellea* studied by him exhibited luminescence under the test conditions but not all in the same degree.

The various isolates of *A. mellea* cultured by the writer have been examined on numerous occasions in comparison with those of *C. tabescens,* which is not known to exhibit luminescence. All actively growing cultures of *A. mellea,* regardless of the source, have agreed in exhibiting luminescence, though in some it was developed but weakly. In all cases the luminescence was confined to the surface mycelium and young aerial rhizomorphs, none being apparent in the submerged rhizomorphs. The entire mycelial mat on the surface of the agar rarely glowed equally throughout, the luminescence usually being stronger at some points than

at others. As the cultures became old and developed a hard, brittle crust the capacity for luminescence diminished or was lost entirely.

On the other hand, pure cultures of *C. tabescens* growing on the same media and under the same conditions have consistently failed to show any evidence of luminescence, though cultures of it and *A. mellea* have been examined together repeatedly in complete darkness. After the lapse of a few minutes to allow the eyes to adapt themselves to the darkness the cultures of *A. mellea,* that have been examined on various occasions, have, with few exceptions, glowed like live coals, while those of *C. tabescens* did not glow at all. Labeled cultures of the two fungi mixed in the dark room could be separated with unerring accuracy on the basis of the presence or absence of luminescence, except for those occasional instances where cultures of *A. mellea* fail to exhibit luminescence. This distinction alone ordinarily will prove sufficient to separate these two closely related fungi in pure culture. It should be borne in mind, however, that cultures of *A. mellea* exhibit luminescence most strongly when young and growing actively and least so when they become old and inactive.

The exhibition of luminescence by the mycelial sheets developed between the bark and the wood and within the inner layers of bark in freshly dug specimens of roots of plants attacked by mushroom root rot, however, while indicative, does not necessarily constitute proof that *A. mellea* is involved. In a few instances Florida specimens that exhibited distinctly luminescent mycelium when examined in the dark, have yielded *C. tabescens* upon culturing and the pure cultures obtained in such cases have consistently failed to exhibit any evidence of luminescence. The same situation was true of the several specimens of mushroom root rot collected at Auburn and Opelika, Alabama. The luminescence of the mycelium in specimens of *Clitocybe* root rot as it occurs in nature appears to be exceptional. Since the fungus after isolation in pure cultures has never exhibited any evidence whatever of luminescence, even though the mycelium occasionally did under natural conditions, it is thought that this phenomenon may at times be due to luminous bacteria associated with the root-rot fungus.

SPOROPHORE PRODUCTION

One of the most striking characteristics of *C. tabescens* is the readiness with which it fruits in culture. Not infrequently the original isolations in small test tubes have developed miniature clusters of mushrooms that matured and shed basidiospores. Fruiting of this fungus usually is obtained readily in large test tube or flask cultures. Some isolates fruit with unusual readiness and others more tardily. As reported by the writer (12), it appears to make no difference in the growth and fruiting of the fungus whether the cultures are started from basidiospores or mycelial transfers. In cultures started from basidiospores it is not unusual for the fungus to produce sporophores and cast spore prints in from 35 to 45 days and this has been accomplished in several cases in one month's time. It is rather amazing that a gill fungus can be carried through its life cycle, with a very limited development of mycelium and rhizomorphs, within such a short time. However, *Lentinus lepideus* Fr., *L. tigrinus* Bull. ex Fr., *Schizophyllum commune* Fr. all develop sporophores in a rather short time in cultures.

Fruiting in test tube cultures, both in the case of original isolations and mycelial transfers from stock cultures, has been accomplished in even less time. An original isolate from Jerusalem-thorn (*Parkinsonia aculeata* L.) developed sporophores that matured and shed basidiospores at the end of 25 days. The same occurred in transfers from isolates from Botree fig (*Ficus religiosa* L.), poinsettia (*Euphorbia pulcherrima* Willd.) and Surinam-cherry (*Eugenia uniflora* L.) at the end of 26, 28, and 29 days, respectively. An even more striking case of precocity of sporophore development was observed in a series of 20 isolates, made in 18 mm. test tubes, from scrub hickory (*Carya floridana* Sarg.) during the winter when growth was greatly delayed by low room temperature. In each of 5 tubes with very scant or no development of rhizomorphs, clusters of small mushrooms formed from the initial mycelial growth before it had begun to spread over the surface of the agar. In two cultures a sporophore matured sufficiently to shed spores in a minimum period of 24 days. In flask cultures, where there is a much greater opportunity for the growth

of mycelium and rhizomorphs, a much longer period usually is required for fruiting. However, when fructification occurs in such cases it is on a much larger scale.

FIG. 5. Culture of *C. tabescens* shown in figure 4, photographed 5 days later to show unusually large number of mature sporophores.

When *C. tabescens* gets ready to fruit a group of little hornlike processes develops at some point on the surface of the mycelial mat and these are the primordia of the cluster of mushrooms. In test

tube cultures usually only a single cluster develops, while in flask cultures from one to several may develop. These enlarge rapidly and soon differentiate into buttons with distinct caps and stems (FIG. 4). In test tube cultures, where there is very little room for development, usually one or a very few of the sporophores that may differentiate in the cluster continue to grow and the rest abort. In some cases all may dry up before maturing. Even in flask cultures, especially when several clusters of embryonic sporophores are differentiated, most of them abort and only a few continue developing. Even when several mushrooms develop for a time, further growth usually is centered in one or two. The largest specimen grown in a 500 ml. Erlenmeyer flask was a single sporophore that prevailed over the others. This developed a cap 7.5 cm. broad and a stem 1.5 cm. in diameter at the largest point but attained this unusual size only by the stem curving so that the cap grew sidewise near the top of the flask. Figure 5 shows an unusual number of sporophores maturing in a flask of this size with none being particularly large. In the great number of cultures that have fruited over a period of several years the sporophores invariably have been typical of *Clitocybe*, with the gills distinctly decurrent on the stem and no sign of an annulus. In both test tube and flask cultures the initial production of sporophores may be followed shortly or within a few weeks by the production of new ones (FIG. 3, A) if the cultures do not become unduly desiccated.

In the writer's cultural work with *C. tabescens* over a period of several years two instances have been noted where sporophores differentiated from the ends of rhizomorphs and both occurred in cultures in test tubes. The origin of sporophores in this manner appears to be very rare for this fungus, though it has been illustrated frequently for *A. mellea*. The first case noted was in a transfer from an isolate from a cherimoya (*Annona cherimola* Mill.). Three rhizomorphs that grew upward through the surface of the agar slant developed 5 miniature mushroom buttons, with two on the upper rhizomorph, two on the next lower one, and one on the lowest one. One of the pair on the end of the middle rhizomorph developed into a mushroom about ½ inch in diameter and shed a good spore print. The other case was an original isolate from a painted copperleaf (*Acalypha Wilkesiana* var. *A. mar-*

ginata Hort.) bush. A cluster of miniature mushrooms developed from the end of a rhizomorph that grew upward near the top of the agar slant. The upper two of these mushrooms matured and shed basidiospores in a little more than a month from the time of making the isolation (FIG. 3, B).

Of the numerous isolates of *A. mellea* from a wide variety of sources cultured along with *C. tabescens* by the writer over a period of several years, none has shown the slightest indication of fruiting, not even on bread. The experience of Richards (**18**) with respect to fructification in these fungi was similar. She readily obtained sporophores from the single isolate of *C. tabescens* which she had but was unsuccessful in getting any of the 6 isolates of *A. mellea* to fruit. Reitsma, who secured and illustrated fruiting in *A. mellea,* mentioned (**11**, p. 505) that it was generally stated that it grew best on bread. In a series of cultures of this fungus made by Lisi (**8**) to encourage sporophore production, only one variant responded of the 10 morphologically distinct ones that were studied. The great readiness with which *C. tabescens* fruits in culture and the total lack of fruiting of *A. mellea* when grown on the same media and under the same conditions clearly demonstrate that these fungi, though very similar in many respects, are quite distinct.

COMPARATIVE INFLUENCE OF TEMPERATURE ON GROWTH

A study was started in June 1937 to determine the comparative influence of 8 different temperatures on the growth of *C. tabescens* and *A. mellea.* In this experiment there were used as sources of inoculum 8 isolates of *C. tabescens* from different hosts from various parts of Florida, 3 of *A. mellea* comprising isolates from California, Pennsylvania, and Wisconsin, and 1 of its tropical analogue, *A. fuscipes,* isolated by Gadd from tea (*Camellia sinensis*). A series of 16 transfers was made from each of these cultures to 1 × 8-inch test tube slants of potato-dextrose-maltose agar, which has proved an ideal nutrient medium for the growth of these fungi. This provided duplicate transfers from each stock culture at each of the 8 temperatures used. These transfers were held until it was apparent that growth was starting in all. They were then placed

in their respective refrigerators and incubators and held for 30 days. These temperatures ranged from 12.3° to 40.1° C., based on the average of the daily readings for the period.

C. tabescens grew at all temperatures used from 12.3° to 35.8° but did not grow at 40.1° C. It made the best and about equally good growth of mycelium and rhizomorphs at 24.7°, 29.0°, and 31.6°. The growth of this fungus was very good at 21.7°, fair at 14.2°, slight to fair at 12.3°, and slight at 35.8° C.

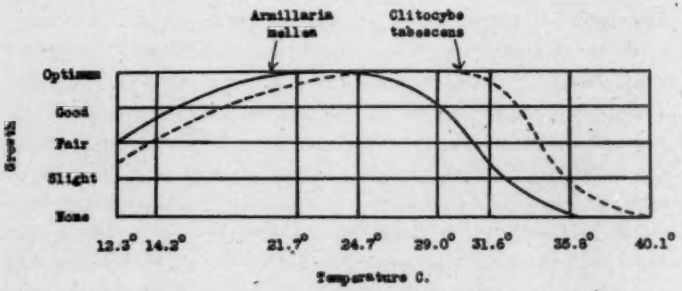

FIG. 6. Graphic comparison of growth of *C. tabescens* and *A. mellea* at different temperatures, showing the distinctly higher range of the former for optimum growth.

A. mellea and its tropical analogue, *A. fuscipes*, behaved essentially the same and grew at all temperatures used from 12.3° to 35.8° but did not grow at 40.1°. They made the best growth of mycelium and rhizomorphs at 21.7° and 24.7°. The growth of these fungi was very good at 14.2°, good at 29.0°, fair at 12.3°, fair to slight at 31.6°, and slight to none at 35.8°. This comparison, which has been expressed graphically in figure 6, shows that *C. tabescens* has a distinctly higher temperature range for optimum growth than *A. mellea*. Exposure to the high temperature of 40.1° C. for 30 days proved lethal to both fungi, as previously reported (**14**), since not a single culture of either revived after being removed from the incubator. The investigations by Wolpert (**21**) and Reitsma (**11**) showed that 15°, and 15–19°, respectively, were less suitable for growth of *A. mellea* than 25° C., which both considered the optimum. Recently, Benton and Ehrlich (**2**), working with 10 isolates of this fungus from western white pine (*Pinus*

monticola), concluded that the optimum temperature for growth in plate cultures lies between 19° and 25° and probably is between 21° and 25° C., the latter range agreeing with the results obtained by the writer.

The apparent absence of *A. mellea* in central and southern Florida and its infrequent occurrence in the northern part of the State in contrast with the prevalence of *C. tabescens* throughout the State as a whole appears to be attributable to the different temperature relations of these two root-rot fungi for growth. *A. mellea* has been found to occur, chiefly saprophytically, in areas of hammock forest around Gainesville but apparently fruits but rarely. It fruited with unusual abundance, however, during the fall and winter of 1937, the prolonged cool weather of the fall apparently sufficing to induce the development of sporophores. In general, *C. tabescens* largely replaces *A. mellea* in Florida and some of the other southeastern States.

COMPARATIVE INFLUENCE OF pH REACTION OF MEDIUM ON GROWTH

Preliminary attempts were made by the writer (**14**, **15**) to determine the effect of the pH reaction of the media on the growth of *C. tabescens* and *A. mellea*. In June 1937, 84 1 × 8-inch test tubes of potato-dextrose-maltose agar with a pH reaction of 6.3 after sterilization were divided into lots of 14 and these lots adjusted by titration to give pH reactions of 3.9, 5.3, 6.3, 7.0, 7.6, and 8.7, respectively. Preliminary tests were run on extra tubes to determine the number of drops of HCl or KOH necessary to add to each tube to adjust to these respective pH values. Each lot of tubes was titrated as necessary, after warming to liquefy, and the tubes agitated to mix thoroughly before cooling. Four isolates of *C. tabescens*, from different hosts from various parts of Florida, and 3 of *A. mellea*, comprising isolates from California, Pennsylvania, and Wisconsin, were used as sources of inoculum. Transfers in duplicate were made from each stock culture for each pH value. These were held for 30 days at room temperatures ranging from 28 to 30° C.

The 4 isolates of *C. tabescens* averaged about equally good growth of mycelium and rhizomorphs at all reactions but there was less tendency to develop sporophores on the alkaline side of the

range. The 3 isolates of *A. mellea* averaged equally good growth of mycelium and rhizomorphs at all reactions from pH 3.9 through 6.3 but produced a progressively decreasing amount of growth beginning with pH 7.0, which is in close agreement with the results secured for the latter fungus by Wolpert (21).

In September 1939, a set of 50 ml. Erlenmeyer flasks of potato-dextrose-maltose agar with peptone were divided into lots of 10 and these lots were adjusted to pH reactions of 4, 5, 6, 7, and 8, respectively, prior to sterilization. In checking after sterilization these reactions were found to have changed to pH 4.2, 5.2, 5.6, 6.4, and 7.1, respectively. A set of 5 flasks with agar of each of these pH values was inoculated with pure cultures of *C. tabescens* and a duplicate set with *A. mellea*, thus making 25 cultures in each series. These flasks were held at room temperatures ranging from 24 to 27° C.

The rapidity of mycelial growth and rhizomorph development varied greatly in the different transfers of both series at the start, irrespective of the reaction of the medium. While all transfers of each fungus were made from a single culture, greater variation occurred in growth from the different transfers than was manifest at the different pH reactions. In the *C. tabescens* series growth at pH 4.2 was retarded at first but equaled that in the other flasks by the end of 4 weeks, when, with the exception of one flask at pH 5.6, the surface of the agar in practically all was covered with mycelial growth and the bottoms with rhizomorphs extending up the sides toward the surface of the agar. In the *A. mellea* series growth at pH 4.2, with the exception of two flasks, also was somewhat retarded in general at first. Growth in this series was less vigorous than in the *Clitocybe* series. At the end of 6 weeks it was apparent that all lots of both fungi averaged approximately the same growth regardless of the reaction of the medium. At the end of this period, when the growth of the cultures began to be checked by desiccation, the majority of the flasks in the *Clitocybe* series had developed masses of embryonic sporophores, whereas none of the flasks in the *Armillaria* series showed any evidence of fruiting.

The foregoing experiments have yielded no particularly striking results with respect to the optimum reaction of the medium for the

growth of either of these fungi, other than to indicate that it apparently is not particularly significant within certain limits and that both have a wide pH range on the acid side of the scale. In his study of *A. mellea*, Wolpert (**21**) found that the pH limits and optimum pH zone varied with the temperature and the medium. At 25° C. in Richard's solution growth was inhibited by pH 2.9 and 6.9 and the optimum occurred at pH 4.9, while in bacto-peptone solution growth was inhibited by pH 2.0 and 7.8 and the optimum occurred at 3.8. With both media, however, he secured a fairly good growth over a relatively wide pH range but this fell rapidly to zero as the neutral point was reached or passed. Reitsma (**11**) secured the maximum growth at pH 5.1 in his series of cultures at the optimum temperature of 25° C. His results also showed good growth over a considerable pH range and he stated that at 25° C. the optimum lay between pH 4.6 and 6.4. In his study of the relation of growth of *A. mellea* to the pH concentration of liquid media 2 relatively slow-growing variants of the 10 morphologically distinct ones studied by Lisi (**8**) showed no conspicuous growth optimum while with others the optimum ranged between pH 4.0 to 6.0. He found that the variants altered the final pH of the nutrient solution in different degrees, some towards the alkaline side and others toward the acid side. However, the amount and the direction of change in the final pH were not correlated with the amount of growth. Benton and Ehrlich (**2**) found two optima for the growth of their isolates of *A. mellea* at 25° C. on malt agar, namely pH 4.5 and 5.5. A pH of 5.0 proved to be the most favorable, and a pH of 3.0 the least favorable, for development of rhizomorphs. Judging by these results, it does not appear that the growth of either of these fungi is sufficiently limited by the pH reaction of the medium to offer any practical application from the standpoint of control measures.

SUMMARY

The taxonomy of *Clitocybe tabescens* is discussed with reference to the assumption by some mycologists not especially familiar with the plant, that it is merely an exannulate form of *Armillaria mellea*. The importance of the isolation of the fungus, in the absence of

sporophores, in the diagnosis of the root rots caused by these respective fungi, especially in regions where both may occur, is indicated.

The root rots caused by these closely related fungi have been found to agree with respect to the symptoms exhibited by attacked plants, general appearance and growth of the mycelial sheets, development of xylostroma outgrowths extruded through longitudinal fissures in the bark of attacked roots, the marked predilection of the fungi for oak roots, and their ability to develop either parasitically or saprophytically. The root rot caused by *C. tabescens* differs, however, in the absence of the black, rounded or flattened, cortical and hypogeal, stringlike rhizomorphs, the perforate character of the younger mycelial sheets and their less fan-shaped type of development at the advancing margins.

Cultural studies of a large number of isolates of these fungi have shown further striking differences, though there was considerable variation in growth and rhizomorph production, as well as in readiness of fruiting in the case of *C. tabescens*, among the different isolates. Considerable variation also occurred frequently in series of transfers from individual isolates in both species. *C. tabescens* consistently made a more rapid growth than *A. mellea*. It usually fruited with great readiness, whereas *A. mellea* never exhibited the slightest tendency to fruit. The aerial rhizomorphs of *C. tabescens* are short and relatively blunt at the tips and remain light-colored; those of *A. mellea* usually are long and needle-shaped and become dark reddish-brown to blackish.

Pure cultures of *C. tabescens* have consistently failed to show luminescence, whereas those of *A. mellea* usually exhibited it more or less strongly, at least when young and growing actively. Moreover, *C. tabescens* has been found to have a distinctly higher temperature range for optimum growth than *A. mellea* (25–30° C. as against 21–25° C.). This appears to account for it largely replacing the latter fungus in Florida and other southeastern States. A temperature of 36° C. was close to the upper limit for growth of both fungi, especially *A. mellea*, and 40° C., maintained for a month, proved lethal to both.

Both fungi in cultures on potato-dextrose-maltose agar exhibited a wide pH range on the acid side of the scale, starting with pH

3.9 in one series and pH 4.2 in another. *C. tabescens* grew well in general at all reactions up to pH 7.1 in one series and pH 8.7 in another but fructification was inhibited on alkaline media, while *A. mellea* appeared to be distinctly intolerant of alkaline conditions and growth diminished rapidly after the neutral point was reached. However, it does not appear that the growth of either fungus is sufficiently limited by the pH reaction of the medium to offer any practicable application from the standpoint of control measures.

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AN ANALYSIS OF THE MECHANISM OF BUDDING IN YEASTS AND SOME OBSERVATIONS ON THE STRUCTURE OF THE YEAST CELL[1]

CARL C. LINDEGREN

(WITH 20 FIGURES)

Budding of yeasts is an extraordinarily unique method of cell division and heretofore no one has elucidated the mechanism. The present study reveals that budding is the direct result of the extension of a tube from the vacuole to a point on the cell wall where a very tiny protuberance is formed on the outer surface of the cell into which the vacuole-tube passes and in which it enlarges to form the bud-vacuole. The following description of the structure of the yeast cell will serve to orient the reader.

THE STRUCTURE OF THE YEAST CELL

The structure of the cell of *Saccharomyces cerevisiae* has been the subject of much dispute, but Wager and Peniston's observations are, in my opinion, the most complete that have been made and my own observations follow theirs closely. Their "text-figure," which summarizes their findings, is reproduced herewith (FIG. 1). Table I lists the designations which they gave the different organelles along with the name applied to the same structures by Guillermond, Janssens and Leblanc, and myself. Wager and Peniston's interpretation was limited by contemporary concepts of cell structure, but their drawings reveal an organization easily understandable in terms of modern concepts of the nucleus. They show that the yeast nucleus has a structure similar to that described by Harper (**1905**) for the Ascomycete, *Phyllactinia*. Attached to one side of the nuclear vacuole is a smaller body which

[1] This work was supported by a grant from Anheuser-Busch, Inc., St. Louis.

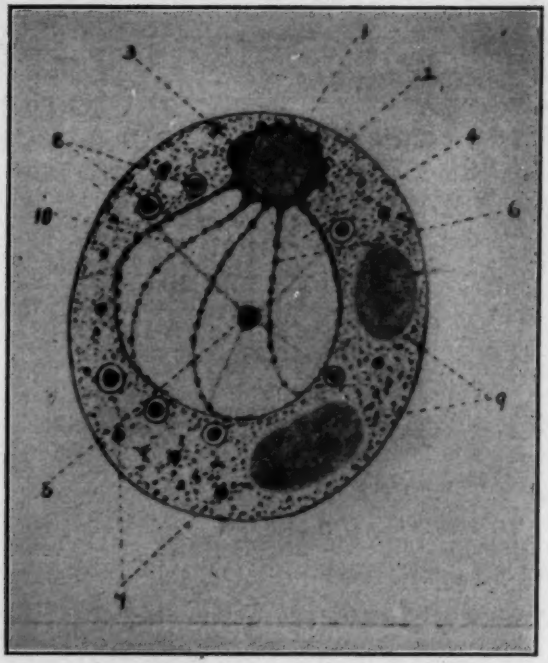

FIG. 1. Yeast cell from Wagner and Penniston.

TABLE I

NAMES OF ORGANELLES IN FIGURE 1 BY DIFFERENT AUTHORS

Wager and Peniston	Guillermond	Janssens and Leblanc	Lindegren
1. Nucleolus	Nucleus	Nucleolus	Centriole
2. Peripheral layer of chromatin			
3. Chromatin patch on one side of nucleolus			
4. Nuclear vacuole	Vacuole	Nucleus	Nuclear vacuole
5. Central volutin granule in the vacuole			Nucleolus
6. Chromatin network			Chromosomes with chromomeres
7. Granules of fatty substance			
8. Volutin granules			Volutin
9. Glycogen vacuoles			Glycogen
10. Delicate suspending threads for the central volutin granule			

is not ordinarily visible in the living cell and which other workers, notably Guillermond (1910), called the nucleus. This structure was called the nucleolus by Wager and Peniston; it corresponds to the centriole in *Phyllactinia* and it has many characteristics of the fungal centriole. The nucleolus is inside the nuclear vacuole and Wager and Peniston called it the "central volutin granule in the vacuole." Wager and Peniston distinguished clearly between the volutin granules attached to the outer wall of the nuclear vacuole, and the chromatin granules (chromomeres) which are inside the nuclear vacuole and borne on chromosomal fibers according to the current conventional concept. The chromosomes are attached to the structure, which I shall call the centriole, exactly as they are in the higher ascomycetes. The large eccentric centriole with polarized chromosomes is characteristic of the fungi. Guillermond probably mistook the centriole for the nucleus because it divides at each mitosis, shows internal structure, and retains hemotoxylin rather firmly.

According to the view presented here, the nucleus is a compound structure containing the hemispherical centriole intimately attached to the nuclear vacuole. Observation of growing cells usually shows that the vacuole is flattened on one side and otherwise is almost a perfect sphere (FIG. 4). The flattened side of the nucleus is the area of attachment to the centriole. The centriole is usually not visible in unstained material but can be brought out by treatment with iodine. On one side of the centriole and about one-fifth its size in some cells, there appears near the juncture of the vacuole and the centriole, another body described by Wager and Peniston as the "chromatin patch." This structure can also be observed in some cells suspended in .01 per cent methylene blue. It stains a faint blue while the vacuole fills with pink dye (FIG. 5).

OBSERVATIONS OF THE CHROMOSOMES

A fruitful method for observing yeasts is to mount them in .01 per cent methylene blue. The dead cells and the living cells stain quite differently. At first the cytoplasm of dead cells stains a light blue. The vacuole of the dead cells later takes on a pinkish tinge and the chromosomes in the vacuole stain a light red. Even-

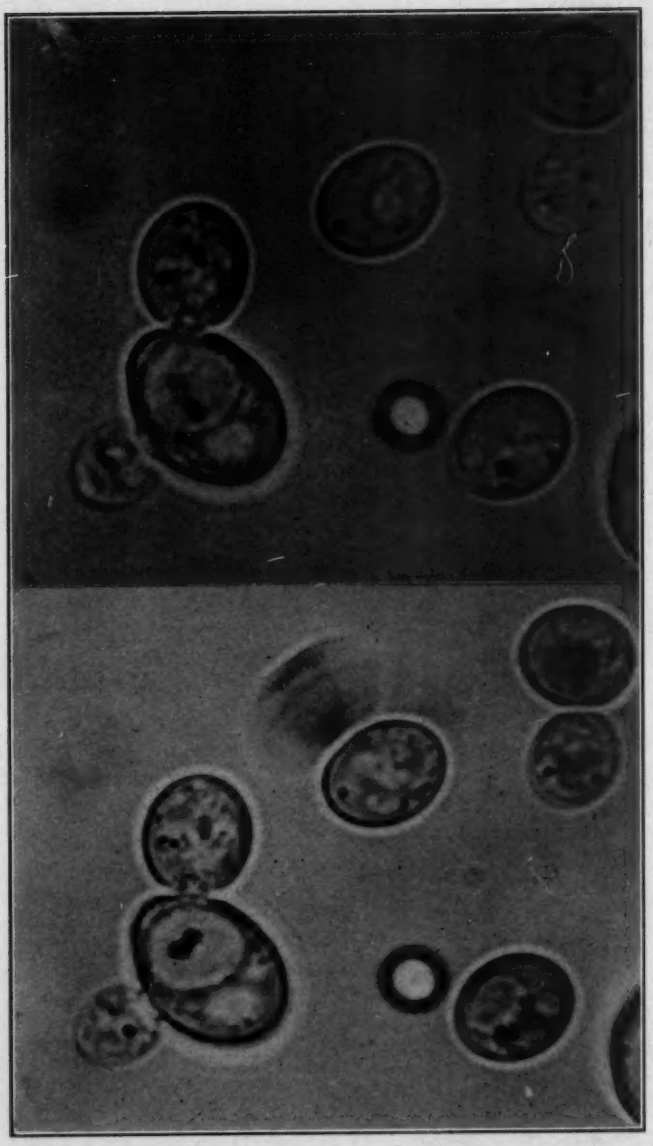

FIG. 3. Yeast Cells.

FIG. 2. Yeast Cells.

tually the dead cells become completely over-stained with methylene blue. However, in the living cells, at the outer edge of the slide or on the border of a bubble, the chromosomes, within the nuclear vacuole, often take on a deep blue color and are clearly visible as small irregular, twisted bodies, sometimes polarized, but usually free and in rapid Brownian movement. In the dead cells the pink nuclear sap is coagulated and the chromosomes are stationary. The stain in the chromosomes of the living cells is evanescent and apparently depends upon the oxidation potential within the cell. From 10 to 20 minutes after they have taken on their intense deep blue they completely disappear under observation, presumably due to reduction of oxidized dye to the leucobase (FIG. 2, 3). This indicates that the methylene blue passes through the highly reduced cytoplasm as the leucobase and becomes oxidized on contact with the surface of the chromosome which probably does not have much reducing power. After the stain disappears it can be brought back by a second addition of the dye. Usually only one or two pairs of chromosomes stain by this method. The chromosomes appear to be paired somatically but critical observations are difficult and each chromosome might be folded back upon itself (FIG. 6, 7). Sometimes several are tangled together in an irregular mass.

On the addition of more dye, the chromosomes may reappear in the vacuole and the dye remains in them longer this time, apparently due to the diminution of the amount of reducing substance in the cytoplasm, possibly because the cells are losing some of their vitality. Sometimes the chromosomes inside the cells ball up into small, tightly-wound bodies that cease their Brownian movement and attach themselves to the inner face of the nuclear membrane. Occasionally the chromosomes seem to be polarized (FIGS. 8, 9) and I have observed the long threads retract toward a single point of attachment at the side of the nuclear vacuole (FIG. 10). The phenomenon has somewhat the appearance of a crystal becoming deliquescent. Eventually one finds either one or more large lenticular blue-black masses appressed to the inside of the nuclear vacuole. Six is the largest number which I have observed in diploid cells. If the chromosomes were paired this would represent the haploid number. In old aniline blue lacto-phenol prepa-

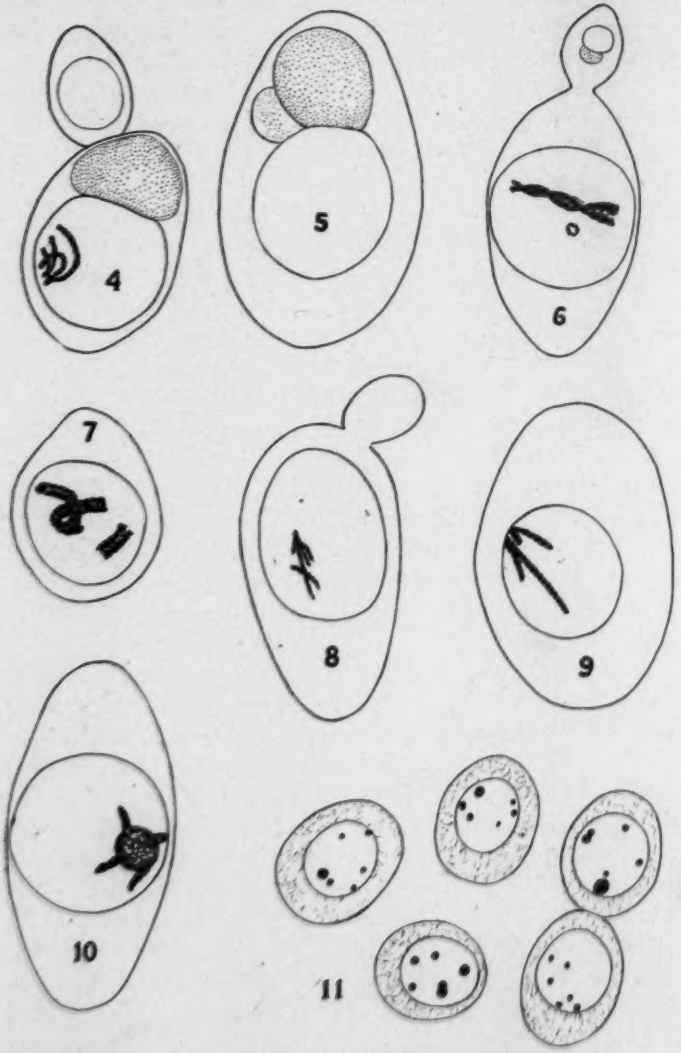

FIG. 4–10. Outline drawings of yeast cells. FIG. 11. Same showing blue staining bodies.

rations the cells contain from one to six clearly defined, light blue bodies inside the nuclear vacuole (FIG. 11) produced by the attachment of the chromosomes to the wall of the vacuole just as with methylene blue. The aniline blue stain is stable. Figure 11 is a drawing reconstructed from photographs.

MOVEMENT OF THE CHROMOSOMES IN THE VACUOLE

When a small drop of aniline blue in lacto-phenol is placed near the edge of a wet mount and allowed to diffuse between the slide and the cover slip, in some of the vacuoles one can observe long, slender, delicately beaded thread-like strands vibrating in the nucleoplasm. These structures do not take the dye but seem merely to change their refractive index (possibly due to action of the acid or the phenol) so that they become observable. Sometimes one larger, thicker strand, possibly produced by the coalescence of several strands, may be seen moving sinuously in the nuclear sap. The strands are usually polarized although this may not always be the case. Even the slender ones seem to be relatively rigid, bending something like a very slender, but rather long thin steel wire. The chromosomes in this condition are only visible momentarily and soon disappear but they resemble Wager and Peniston's figures closely enough to constitute confirmation of their observations. In the case of their preparations fixed with $HgCl_2$ and subsequently stained, the chromosomes are attached to the inner surface of the nuclear vacuole and are motionless. $HgCl_2$ apparently prevents the "balling up" of the chromosomes which occurs when living preparations are treated with methylene blue or aniline blue.

These observations indicate that the chromosomes in the living cell vibrate in the nuclear sap. After one has observed the phenomenon in cells in which the refractive index of the chromosomes makes them unmistakably visible, suggestions of the movement are visible in other yeasts such as *Torula utilis*, *Saccharomycodes ludwigii*, and *Schizosaccharomyces octosporus*. The motion continues after flooding with Lugol's iodine which stains the glycogen brown and often brings the chromosomes into higher relief. The vibration of the chromosomes should greatly facilitate

the exchange of materials between the nuclear sap and the cytoplasm.

While the lacto-phenol is diffusing into a wet mount some of the cells in its path reveal a large number of smaller bodies in active Brownian movement in the nucleoplasm paralleling observations which I have made on moribund yeast cells. These particles have not been identified. In some unstained yeast cells I have observed similar small bodies inside the nuclear vacuole in rapid continual motion. Their activity is strongly reminiscent of the movements of a flock of midges hanging in the summer air. The motion is too rapid to permit counting although estimates of from 30 to 60 may be made. They are all about the same size and are evenly suspended throughout the nuclear space, while the nucleolus or the "balled up" chromosomes (one cannot tell which) moves sluggishly on the floor of the nuclear vacuole in low focus. In some cells the sluggish body is not apparent. This phenomenon is observable in about 10 per cent of the cells of several special strains of *S. cerevisiae* after the cultures have been grown in broth for a few days.

Badian found that the structures, which I have called the centriolar bodies, take the Feulgen stain and this has been confirmed by Dr. Hampton Carson and Miss Lillian Nagel (unpublished, personal communication). However, chromosomes are structures which perform a specific biological function rather than specific chemical compounds and the morphological evidence described in this paper indicates to me that the general rules concerning the specificity of the Feulgen stain for chromosomes do not hold in yeasts.

THE DIVISION OF THE CENTRIOLE

Badian (**1937**) developed an exceedingly effective stain for bacteria and fungi. He killed the cells with osmic vapors, stained with methylene blue and destained with eosin. He studied mitosis and meiosis in *S. cerevisiae* and stated that the cells contained two chromosomes which divided by longitudinal splitting. However, his figures show that the so-called chromosomes always pull apart finally by thinning out at the middle and the final separation is by a crude transverse fission. Furthermore, he stated that the haploid

chromosomes fuse end to end to form the diplophase, rather than associating to form a pair of chromosomes according to the usual method. If his conception is correct the number of chromosomes in haplophase and in diplophase would be the same. The life cycle as described by Badian is shown in figure 12 copied from his paper.

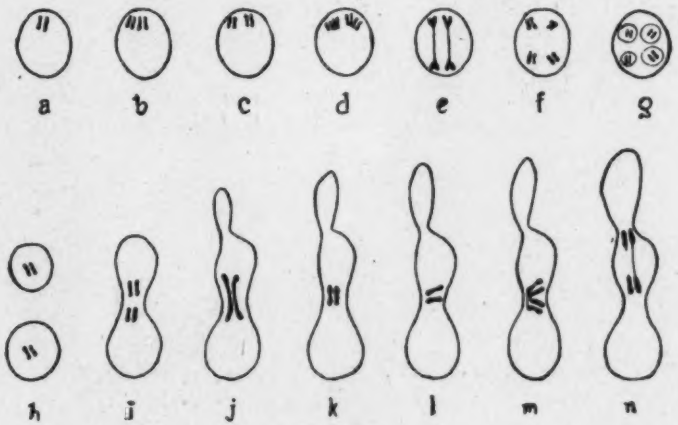

FIG. 12.

The structure which I have called the centriole contains two rod-shaped bodies which stain well with aceto-orcein and divide by a crude transverse fission. They are the only bodies in the cell which take this stain and they are undoubtedly the bodies described by Badian as the chromosomes. Badian concluded that at copulation the chromosomes fuse end to end to produce the diplophase. However the vacuoles also fuse at that time and it seems more probable that he actually observed the fusion of the rod-shaped components in the centriole rather than of the chromosomes themselves. Harper (**1905**) proved that fusion of the nuclei in *Phyllactinia* is initiated by contact of the centrioles, although his techniques did not reveal any internal structure in the centrioles. If the fusion of the nuclei in yeasts were initiated by end to end fusion of the centriolar bodies, the anomaly described by Badian in which a diploid chromosome is supposedly produced by the end to end fusion of two haploid chromosomes would be explained.

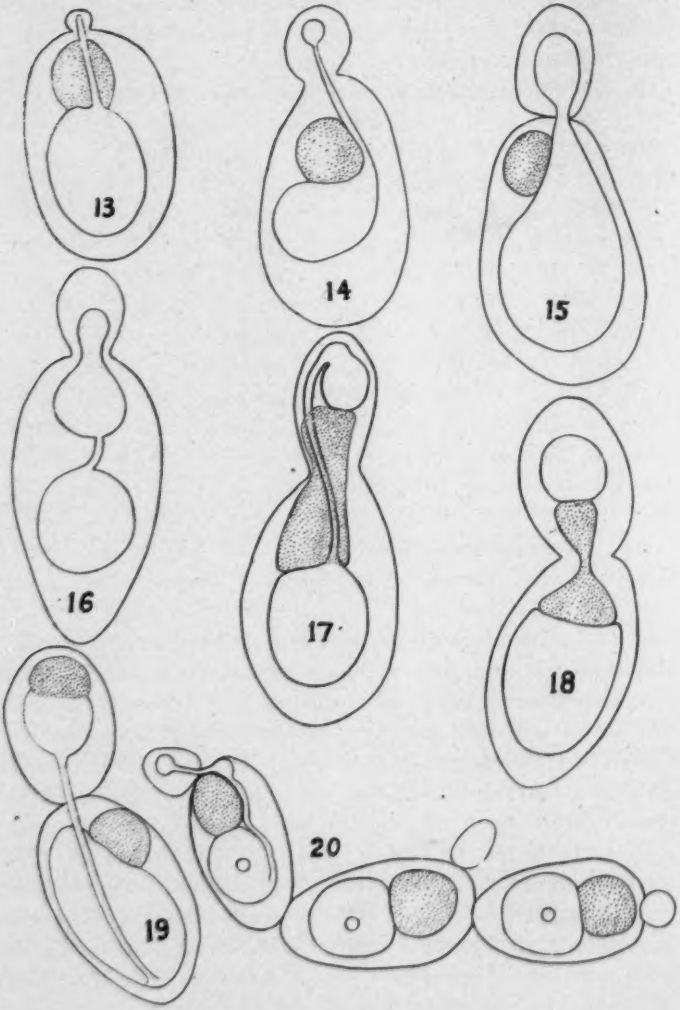

FIG. 13–20. Outline drawings of yeast cells.

BUDDING

When a yeast cell buds both the nuclear vacuole and the centriole divide. The first step is the formation of a long slender tube leading from the vacuole to the periphery of the cell (FIG. 13). This phenomenon can only be observed in cells containing enough glycogen so that the iodine stain delimits the vacuole and its tube as a clear space in the surrounding reddish brown cytoplasm. Observation is facilitated by the use of a Wratten 45 filter which converts the reddish brown color of the cytoplasm to blue-black and reduces the chromatic aberration of the lens system. The canal from the vacuole may begin any place on the surface of the vacuole, but usually appears at a point near the attachment of the vacuole and the centriole (FIG. 13, 14, 15, 17). The bud is always produced near the centriole and when the canal emerges at the opposite side of the vacuole, the long, slender channel extends all the way from the most distant part of the cell through the cytoplasm and finally produces the bud near the centriole (FIG. 19, 20). Occasionally the bud-opening is too small to permit the contents of the vacuole to enter the bud and the canal is distended at this point like the oesophagus of an ostrich swallowing an orange (FIG. 16, 20). A bulb is produced at the end of this canal to form the bud-vacuole (FIG. 14, 15, 17, 19, 20). During this period the centriole is a hemispherical solid unyielding structure that is not deformed by movements of bodies near it. After the bud-vacuole is formed the centriole divides (FIG. 17, 18, 19). Sometimes in the Lugol's solution, it is seen as two bodies which appear to divide by stretching out and thinning out at the center. After the division of the centriole is completed and the establishment of contact of bud-vacuole and bud-centriole has been attained, the interconnecting canal between the mother and the bud-vacuole disappears.

As soon as the bud approaches the size of the parent cell, the nuclear apparati in bud and mother cell reorient themselves so that the centriole in each cell is distal to the bud partition. This is easily observed in single pairs of cells and is also seen in the first two cells of the chain in figure 20.

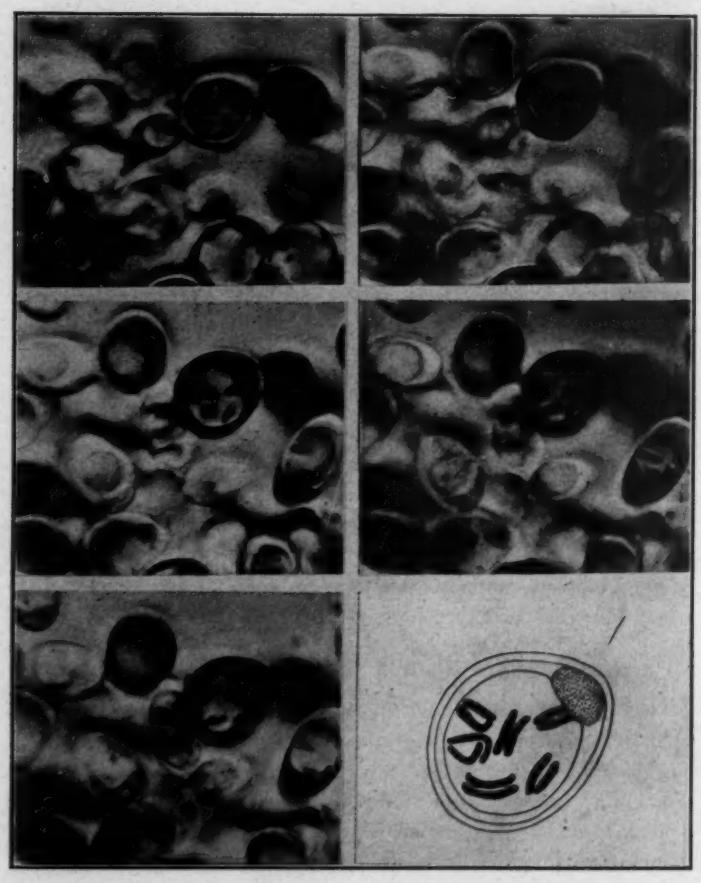

FIG. 21. Yeast cells showing chromosomes.

SUMMARY

The ability of yeast cells to reproduce by budding has distinguished them from other fungi as well as from other organisms and the observations presented here show that the mechanism is quite unique. The nuclear vacuole puts out a slender tube which forms a small protuberance on the cell wall and as the bud grows an en-

largement in the end of the vacuolar tube produces the bud-vacuole.

Observations on unstained cells confirm Wager and Peniston's concept of the structure of the yeast chromosomes and reveal that the polarized chromosomal threads vibrate in the nucleoplasm.

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EXPLANATIONS OF FIGURES

FIG. 1. A drawing copied from Wager and Peniston, showing their interpretation of the structure of the yeast cell.

FIG. 2, 3. Two photographs taken within a few minutes of each other, one of which shows chromosomes in the vacuole in Brownian movement. The other, taken a few minutes later, shows how the dye has faded from the chromosomes.

FIG. 4, 5, 6, 7, 8, 9, 10, and 13 through 20. Outline drawings showing the vacuole and its processes in yeast cells. The centriole, when visible, is stippled. Discussion in text.

FIG. 11. Drawings showing the blue bodies inside the nuclear vacuole found in aniline blue lacto-phenol preparations. These drawings have been reconstructed from photographs taken through several foci. The cells showing the largest number of chromosomes were chosen.

FIG. 12. Yeast life cycle as described by Badian. This figure is copied from his paper showing spore formation from the diploid cell (a-g), and the fusion of two haploid cells to reconstitute the diploid (h, i, j). Arguments are presented in the present paper suggesting that these bodies are not the chromosomes as Badian had thought, but components of the centriole.

POSTSCRIPT

An especially clear toluidine blue preparation has confirmed the above suggestion that yeasts contain 12 somatically paired chromosomes. The five photographs shown in figure 21 were taken

through five different optical levels of a cell. The first shows a pair of central chromosomes, the second and third a pair at the extreme right of the cell, and the fourth shows four other pairs of chromosomes, with single mates revealed in the fifth. The drawing is a reconstruction of the entire cell with the centriole stippled in at the position where distortion of the vacuole and the cell wall has revealed its presence.

A NEW SPECIES OF LYSURUS

W. C. Coker

(with 6 figures)

In June 1945 there appeared in a "soil table" in the botanical laboratory of Clemson College, S. C., an ample colony of a very small phalloid. The table contained local garden soil mixed with imported sphagnum of origin now unknown. The material as brought to us consisted of 16 expanded plants and 9 buttons, mostly single, a few with volvas superficially fused. We describe it as follows.

Lysurus pusillus sp. nov.

Mature plant 1–1.5 (2.2) cm. high, color of volva and stipe dull white, gleba dark brown with a faint tint of olive, odor fetid but not strong; button subspherical, 4–6 mm. thick, largely covered with soil particles, attached at base by one to several strong white, ropy strands which soon branch into a delicate complex, or by more delicate and numerous filaments. Stipe 7–18 mm. high, 2.5–3.5 mm. thick, terete, attenuated below, surface delicately wrinkled, hollow, wall about ⅔ mm. thick, very uneven within, the flesh chambered with a single row of irregular cavities, not constricted above, where it divides into 3–4 (5) bluntly pyramidal, entirely separate, but closely folded, vertical or irregular curved arms which may or may not form a regularly pointed apex, the arms bluntly ridged on the back, the ridge with a shallow central furrow that broadens below and is continuous with the stem; arm surface entirely covered both within and without, except for the ridge furrow, and a little of the base on the inner surface, with irregular, horizontal wrinkles which support the gleba, these folds and gleba running over the apex of the stipe between the bases of the arms so as to connect them. Gleba dark brown with a faint tint of olive, firm, smooth, the tramal cavities as usual very small and irregular. Basidia multi-

spored (up to 8 seen), long, narrow, tapering below and narrowed above; spores elliptic, 1.8–2 × 3.7–4.4 μ.

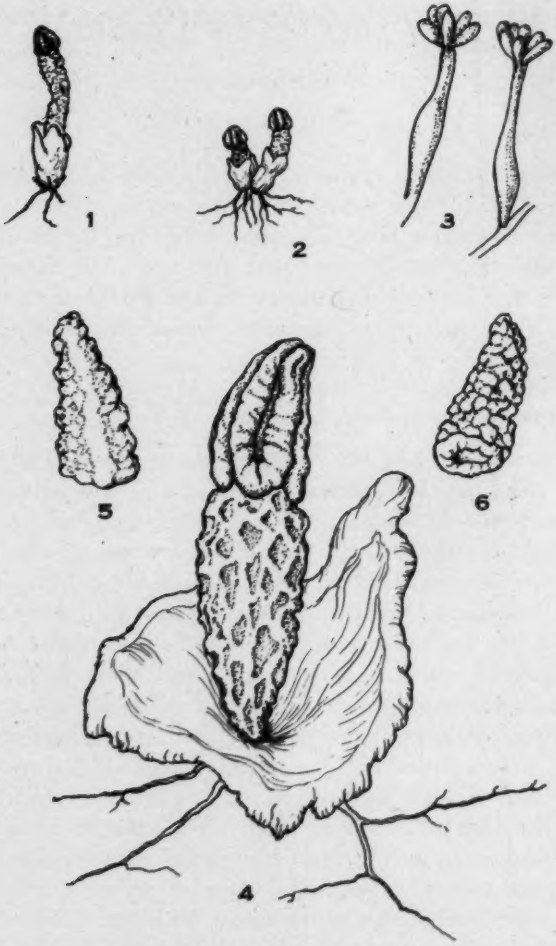

FIG. 1–6. *Lysurus pusillus.*

Receptaculo parvo, 1–2.2 cm. alto; volva subglobosa, pallida; stipite alba, 7–18 mm. longa, tereti, apice non dilatato et diviso in lobos 3–5, lanceolatos,

subacutos, rugosos, apicibus non connexis; gleba ante liquefactionem lobos includente et plane celante; sporis ellipticis, 3.7–4.4 μ longis.

Distinguished by small size, lack of color and arms which are free at the tips and, on first expanding, completely embedded in the gleba.

Types are placed in the Herbaria of the University of North Carolina, Clemson College, and Harvard University.

Single or caespitose in garden soil mixed with sphagnum, Clemson College, S. C. D. B. Rosekrans and A. E. Prince, Coll. June 14, 1945.

This is one of the smallest known phalloids. It seems nearest *Anthurus cruciatus* (Lepr. & Mont.) Ed. Fischer which also is pallid and about the same size, but if that is correctly described and drawn it could not be the same plant. The gleba is figured as a ball embraced by the exposed arms, which indicates the genus *Anthurus,* where it is placed by Fischer. (See Montaine: Ann. Sci. Natur. 3rd Series. Vol. **4**: 360. *Pl. 14, fig. 1.* 1845, as *Aserophallus cruciatus,* and Fischer: Natur. Pflanzenfam. Band **7a**: p. 92, *fig. 66 H.* 1933.) It was found on rotten wood in French Guiana about 100 years ago and so far as we know has not been reported since. Lloyd says the types are preserved in Paris. (Syn. Known Phalloids, p. 40, *fig. 44.* 1909.)

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EXPLANATION OF FIGURES

FIGS. 1 and 2. Three plants, one the largest found. Natural size.
FIG. 3. Basidia and spores. × 1080.
FIG. 4. Young plant, with volva torn open, and with stipe not fully extended. The gleba has been washed off to show the arms. × 6.5.
FIG. 5. Tip of an arm, showing inner side. × 9/100.
FIG. 6. The same showing outer side and central furrow. × 9/100.

Figure 3 is by the writer, others by Alleda Burlage.

FURTHER REMARKS ON MYCOGENETIC TERMINOLOGY

(CONCLUSION)

B. O. DODGE

(WITH 9 FIGURES)

Zickler's diagrams (**1934**, p. 585) are confusing because of the typographical errors in two of his figures. These diagrams are reproduced here in our figures 1, 2, with the errors corrected. The symbols ♀♂ and ♂ have been added by the writer. Zickler holds that the reaction group factors *A* and *a* represent sterility factors and not factors which govern the development of ascogonia and spermogonia. In any event, whatever the *A* and *a* reaction groups do represent, every one will agree that they are not tied up with the production of "sex" organs in this or similar cases. The symbol ♂ means that the race, as cultured, produced many spermatia, although in this paper Zickler (**1934**) admits that some incipient ascocarps are occasionally produced by his *lan* races. ". . . die *lan* Stämme keine oder nur ganz vereinzelte weibliche Geschlechtorgane ausbilden." The *bulb* races form both ascogonia and spermatia and so are represented by the symbol ♀♂.

Comparing figures 1 and 2 below we see, as Zickler pointed out, that he did not have in *Bombardia* the tetrapolar type of reaction such as exists in certain mushrooms (FIG. 2). But, he suggests, p. 585, if a *bulb* race *should* lose completely its power to form spermogonia, then he *would* have an example of tetrapolarity. So, in a later paper (**1937**), and without reporting any additional culture experiments as a basis for his statement, he says there *are bulb* races that do not produce spermogonia. Figure 3 would then picture the situation in such a case. The writer believes, judging from the results of his breeding experiments with *Neurospora* and especially with *Pleurage anserina* (**1935**), that "♀" races of *Bombardia* could be developed. One wonders why Zickler did not analyze the progeny of such a cross as shown in this figure 3.

Hansen and Snyder (**1943**) reporting their culture work with *Hypomyces solani* f. *cucurbitae* present in their diagrams, p. 421, essentially the same condition as that described by Zickler (**1904**) for *Bombardia*. They do not, however, indicate that they had races of the reaction group *a* that are female, ♀. Their theory of the "dual phenomenon" which now calls for a *mutation* from C to M or from hermaphroditic ⚥, to male, ♂, would probably rule out such a possibility in their *Hypomyces*. Furthermore, their definition of sex must be interpreted, having in mind their conclusion: "Any part of a living thallus, ascospores, conidia or bits of mycelium can act as the male fertilizing element." This brings up the question as to the real nature of the microconidia of *Fusarium* or, for that matter, the microconidia of any other fungus. Is any conidium to be classed as a spermatium and therefore male, ♂, if it can act as a fertilizing element? Or is a conidium a spermatium and male only when it is small? Why is it that authors discussing maleness and femaleness in the fungi so often avoid referring to the situation in species of *Neurospora*? Are the tertiary conidia of *Neurospora* spermatia? They are just as small as are the bona-fide spermatia and they function in the same ways.

Zickler (**1934**, p. 583) proved very clearly that the wall of the ascocarp is neither a hybrid structure nor a mixture of tissues to which both of the haploid parental races contributed. The mycelium and primordia of race *viridis* are greenish. Race *rubiginosa* has reddish-brown mycelia and primordia, and race *lactea* is whitish. Regardless of the source (color) of the race from which the spermatia were obtained for spermatization the color of the mature perithecia was always the same as was that of the mycelium and primordia spermatized. Hansen and Snyder (**1943**) in their figure 2 show that the same principle holds for their *Hypomyces*.

The writer was unable to obtain from Zickler cultures of his *Bombardia* for study. That author did not carry on his genetic work to test out his ideas on sex and sterilities. The questions we want answered would include: Are there factors or genes for antheridia and factors for ascogonia? If so, are these allelic, and where are they located on the chromosomes and on which chromosomes? One should not resort to those hypothetical "realizers" or "determiners" unless those F and M genes are located, especially

with reference to those heritable genes governing phenotypic differentiations of "sex" cells. When a ♂ mutates to a ♂ race in *Hypomyces* or to a female, ♀, race in *Bombardia*, what is the gene picture before and after the mutation?

Above all Lindegren (**1936**) has given us a six-point sex chromosome map for *Neurospora crassa*, a sex chromosome map based on the idea that the $+/-$ or A/a relation is a sex-reaction or a mating type relation. Would it be out of place to insist that, from now on, authors in attempting to explain maleness and femaleness in the fungi give us, as Zickler, for example, has done for *Bombardia*, accurate illustrations of the structures which they classify as male or female. One wonders if Hüttig (**1935**) really expected any one who had ever studied sexual reproduction in Ascomycetes to take his illustrations of the oögonium and antheridium of *Glomerella* seriously.

Another thing, should not our future mycogeneticists volunteer to make the races on which they have based important conclusions available to others for study in case it seems desirable to have one's work confirmed by an independent worker? It would throw much light on the nature of reproduction and inheritance in the Ascomycetes if some one would prove absolutely that there exist or could be developed races of *Bombardia, Neurospora, Pleurage* and *Hypomyces*, for example, that are stable "male" races as well as stable "female" races. Then show where on the chromatids the factor complexes for ascogonia and spermatia are located and how they are or are not linked with the $+/-$ or the A/a mating type factors.

In suggesting such experimental studies the writer is not attempting to be facetious. On the contrary, he believes that the development of morphological structures such as ascogonia and spermogonia is governed by heritable genes or gene complexes. Zickler as noted above would have us believe that his ♂ race *bulb* mutates to a ♀ *bulb* race, while Hansen and Snyder (**1943**) appear to believe the reverse mutation ♂ to ♂, or C to M, is the rule. They do not discuss either Zickler's work on *Bombardia* or for that matter the work of Lindegren and others on *Neurospora*. After having studied sexual reproduction in *Ascobolus carbonarius* and *A. magnificus* and having seen those striking and highly differentiated ascogonia and antheridia it would be impossible for the

writer to lose interest or faith in the part such structures play in reproduction and inheritance.

Figures 4–9, following Zickler's scheme, may help to visualize "sexual reproduction" in these heterothallic fungi from two quite different standpoints. First, maleness and femaleness always imply phenotypic morphological sex-cell differentiations. Second, the more fundamental principle of sexuality is that which applies to the simplest as well as to the most complex forms. This implies physiological genotypic sex-reactions or mating type, $+/-$ or A/a, segregations. We see this best exemplified in the heterothallic yeasts, smuts, mushrooms and Mucorales. It also operates in exactly the same way in *Ascobolus*, *Bombardia* and *Neurospora*, for example, where differentiation of "sex organs" occurs sooner or later. In figures 1–9 solid lines indicate positive results or production of ascocarps, dotted lines indicate negative results.

The mycelium of *Neurospora tetrasperma* is normally mictohaplontic or heterocaryotic. Each of the two components when separated normally can be induced to develop ascogonia and spermatia, so that from this standpoint the *A* and *a* component mycelia are both hermaphroditic, ♂♀, just as in the normal heterocaryotic mycelium itself. If we grow these two components together mixed in tube cultures the results are depicted in figure 4. In *Spirogyra* the cell that sends its nucleus out through the conjugation tube is, to the differentiationists, male, ♂; the cell in which the zygospore is matured is female, ♀, as indicated in figure 5. If we now grow our *A* and *a* component races in a plate culture (FIG. 6), the perithecial distribution pattern is such that, on the *Spirogyra* basis, the *a* race is male, ♂, and the *A* race is female, ♀. Figure 7 brings out the relationship.

Gelasinospora tetrasperma is much like *Neurospora tetrasperma*, except that in the former all races, both mictohaplontic and unisexual, are female, ♀, spermatia are not as yet known. For the perithecial distribution patterns which are the same for the two species, see Dodge, 1931, pl. 7, fig. 17 and 1935, pl. 39. Figure 8 diagrams the situation in the *Gelasinospora* from the viewpoint of morphological differentiation of sex organs, while figure 9 follows in line with sex differentiation based on the criteria for maleness and femaleness in *Spirogyra*.

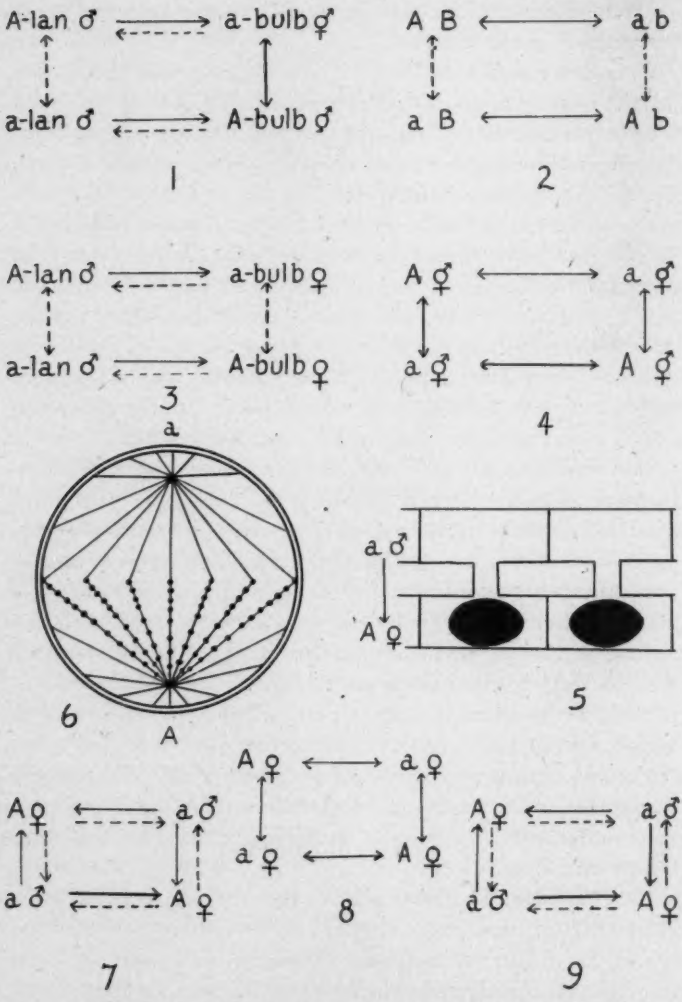

FIG. 1. *Bombardia.* Diagram, adapted from Zickler (**1934**), showing the reactions between races *A* and *a* as related to morphological differentiations of ascogonia and spermatia by the races involved; 2. Tetrapolar sexuality in a mushroom; 3. Reactions between mutant races of *Bombardia;* 4. *Neurospora tetrasperma.* All normal races potentially hermaphroditic, sex-reactions independent of sex-cell differentiations; 5. Male ♂ and female ♀ cells

If the reader is somewhat confused as to the meaning of the diagrams in terms of sex, he should remember that his confusion may be due largely to our use of the symbols for male, female and hermaphrodite, and to the bringing into the discussion morphological differentiations which are often entirely secondary and not primary factors which determine whether or not two races of a heterothallic species will react sexually in reproduction. If one is carrying out genetic studies for the purpose of locating those genes or factor complexes which govern the development of ascogonia and antheridia, and for finding out how such genes are linked and how they are segregated at meiosis, then the symbols would certainly serve a very useful purpose. In such cases we must have, as noted previously, adequate illustrations of those structures which the author would call male or female. One source of confusion has always been the insistence of an author that if a certain structure *acts* as male it is, in fact, male; and so with female.

Zickler (**1937**, b) evidently had not seen the paper on *Pleurage anserina* (Dodge, **1936**). Races No. 5, 9 and 19 never produce spermatia. Figure 1, B, in that paper, illustrates how a race which produced no spermatia yet could "act as male" by supplying nuclei which migrate over to the receptive race. These striking perithecial distribution patterns and the variability with which races produce or fail to produce spermatia and perithecial primordia indicate that those who will undertake a thorough genetic study of this species will be well rewarded because abundant evidence can be unearthed to support almost any theory of sexuality. *Neurospora tetrasperma* is still better because its spermatia, "male, ♂, sex organs," germinate and go on to make normal mycelia. One thing stands out above all else, namely, regardless of where one finds the latter species, Surinam, Australia, Puerto Rico, Texas or the Canal

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of a heterothallic species of *Spirogyra*. We are assured that a cell is male if its nucleus migrates over, and the cell receiving this nucleus and forming the zygospore is female; 6. Diagram of perithecial distribution pattern in plate culture, the sexuality, male ♂ and female ♀, determined by the direction of nuclear migration and production of fertile ascocarps; 7. Diagram of a plate culture following Zickler's schemes; 8. *Gelasinospora tetrasperma*. All races morphologically female, but sexual reproduction is the result of reaction between sex-reaction or mating types *A* and *a;* 9. Diagram interpreting perithecial distribution pattern in terms of sex in *Spirogyra*.

Zone, the species is facultatively heterothallic, and the component races in every case fall into the same two sex-reaction groups, $+/-$ or A/a. This reaction is not only intraspecific but also *interspecific*. True heterothallism in the fungi and algae is of the same nature as it is in Blakeslee's Mucoraceae. It is primarily based on the principle of segregation of genes or gene complexes which regulate the events leading up to and including the sexual fusion of nuclei to form zygotes.

THE NEW YORK BOTANICAL GARDEN

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NOTES AND BRIEF ARTICLES

ANNOUNCEMENT

Mycologia's New Editor-in-Chief

When Mycologia was adopted as the official organ of the newly formed Mycological Society of America, two editorial positions were provided for, an Editor-in-Chief, to be selected by the Editorial Board from among their number to take care of the editorial work of the journal, and a Managing-Editor, appointed by the New York Botanical Gardens to look after its financial interests. Up to the present time, the two positions have been handled as one. It seems expedient now to separate the duties of the two offices. This is a rather delicate surgical operation, but it is hoped the patient will survive and suffer no serious shock.

The Editorial Board has approved the appointment of Dr. Alexander H. Smith of the University of Michigan as Editor-in-Chief, his duties to be taken over in January 1946. Dr. Smith seems to be well qualified both as to training and location in one of the outstanding mycological centers of America. All manuscript for publication in Mycologia should be sent to Dr. Smith.

The writer will continue to act as Managing-Editor for a time at least. I am sure the Mycological Society will give Dr. Smith the loyal coöperation and support which I have had during my term of office. Our best wishes are extended to the new Editor-in-Chief.—Fred J. Seaver.

A Manual of Soil Fungi [1]

The above named volume by Joseph C. Gilman has recently appeared. As stated by the author, this is largely a compilation of material previously published in scattered literature for which there has been much demand. To supply the demand its publication in book form seems warranted.

[1] The Collegiate Press Inc., Ames, Iowa.

The fungi are taken up essentially in the order in which they are treated by Engler and Prantl in "Die natürlichen Pflanzenfamilien" with some variation to fit more modern treatments.

It is needless to say that such a compilation cannot be in any sense complete but lists those forms which the author himself has actually encountered. The book is intended to be used as a guide to others who may wish to continue the study of the microörganisms of the soil and their functions which have not been fully appreciated.—FRED J. SEAVER.

WOLF'S AQUATIC OÖMYCETES OF WISCONSIN [1]

The introduction presents a summary of the more important taxonomic works on the Saprolegniaceae. This is followed by descriptions of the orders, families, genera, and species of Oömycetes found in Wisconsin by the author and by former workers. Twenty-two genera with fifty-five species are included. The descriptions are particularly well written, and the illustrations, some original and others copied, will be helpful to subsequent students in identifying the Oömycetes.—JOHN N. COUCH.

FISTULINA IN FLORIDA

I never expected to record the Beefsteak Mushroom, *Fistulina hepatica* Fr., for Florida, but Dr. G. F. Weber collected it on Aug. 19, 1945, near Keystone Heights, on the road to Camp Blanding. It grew in sandy soil in a thicket of scrubby live-oaks, doubtless attached to buried wood. The spores were pure hyaline under the microscope when fresh, smooth, ovoid, uniguttulate, about 4–5 × 3 μ. The best treatment of this genus is probably in Atkinson's "Mushrooms," pp. 186, 187, where colored illustrations are given of both *F. hepatica* and *F. pallida*.—W. A. MURRILL.

ABORTIPORUS SUBABORTIVUS MURR. IS VALID

In "Lloydia" for June, 1945, Dr. Rolf Singer makes *Abortiporus subabortivus* Murr. a synonym of *Daedalea philippinensis* Pat. A glance at the differences given below will show that the

[1] Wolf, F. T. The Aquatic Oomycetes of Wisconsin, Pt. I. 64 pp., 6 pls. The University of Wisconsin Press, Madison, 1944.

two are distinct. In Patouillard's species the pileus is azonate, cream to fuscous; stipe 8 cm. long, glabrous, appearing varnished; spores 7–9 μ long, echinulate. In my species the pileus is zonate, rosy-isabelline; stipe 4–6 cm. long, not appearing varnished, its surface spongy and finely tomentose; spores 5–6 μ long, minutely roughened. See Bull. Torr. **65**: 655. 1938 for complete description.—W. A. MURRILL.

BOLETUS TABACINUS Peck

In Mycologia **36**: 362. 1944, Dr. Singer states that my *B. pisciodorus* is not distinct from the above but he probably did not have the two types together on the same table as I have now. In *B. tabacinus* the tubes are collapsed and umbrinous, the spores a dark yellowish-brown; in *B. pisciodorus* the tubes are firm, not at all collapsed, larger and fulvous, the spores hyaline under the microscope. Age may make some difference but hardly that much. Peck's species grew in red clay on the bank of a roadside ditch; mine under hickories, oaks, etc. in moderately moist sandy soil among grasses and weeds. The latter has a decided fishy odor at maturity and in drying. Perhaps someone in Alabama can find more of Peck's species and note its odor and the color of its fresh spores. I am indebted to Dr. House for the loan of the type and to Dr. Seaver for specimens collected in Alabama by Earle on Sept. 6, 1899.—W. A. MURRILL.

KARLING'S SIMPLE HOLOCARPIC BIFLAGELLATE PHYCOMYCETES[1]

This book is the second of a series of lectures presented to graduate and research students of mycology at Columbia University on the origin, development, phylogeny, and evolution of the lower organisms. The first book described the Plasmodiophorales, and the present one includes the biflagellate Phycomycetes exclusive of the Leptomitales, Saprolegniales, and Peronosporales. This admittedly heterogeneous assemblage includes about eighty species, twenty genera, and five families, for which the author suggests the group name of Holobiflagellomycetes.

[1] Karling, J. S. Simple Holocarpic Biflagellate Phycomycetes. 123 double column pages, and 25 plates. Published by the author, New York City, 1942.

The introductory chapter reviews the historical background justifying the separation of the simple biflagellate species from the Chytridiales. A separate chapter is devoted to each of the five families, Woroninaceae, Ectrogellaceae, Olpidiopsidaceae, Sirolpidiaceae, and Lagenidiaceae, in which the family characteristics are fully discussed and all the genera and species are illustrated and described, including even the ones whose phylogenetic positions are doubtful or which are inadequately known, a practice which will be very helpful to future workers. However, these chapters are by no means solely taxonomic, for the morphological, cytological, and other literature is also completely reviewed and summarized. Chapter seven is devoted to an impartial discussion of the relationships of the Holobiflagellomycetes to the lower forms, as *Proteomyxa,* on the one hand, and the higher forms, as the Saprolegniales, on the other. The author's viewpoint is expressed as follows: "Present day evidence suggests very strongly that most of these Holobiflagellomycetes are either remotely or closely related to the higher Phycomycetes. However, it is not clearly evident whether they are primitive or reduced and degenerate. . . ." The final chapter is a valuable summary of hosts and bibliography.

The book contains some typographical errors most of which, however, are trivial and detract only slightly from the beautifully smooth and easy-flowing style. In Chapter 2, Zopf's important paper on *Woronina glomerata* is omitted from the bibliography. On page 116 the reference to this paper is given twice: "heft" 2 is given when it should be heft 4, and in the first reference the name of the journal is wrong. The illustrations are well executed, but the author omitted the magnifications of all the figures and the source and explanations of some are left out.

This book, by one of the world's authorities on the lower fungi and related organisms, will be of great service to students and investigators in mycology and hydrobiology.—JOHN N. COUCH.

A CHANGE IN GENERIC NAME

In Mycology **31**: 371. 1945, the generic name *Whetzelia* was proposed by the writer to include the much confused species

Urocystis Waldsteiniae Peck or *Ustilago Waldsteiniae* Pazsche. Since publication it has been discovered that in 1934, Chardon and Toro had already used the generic name *Whetzelia* for a new genus of the Sphaeriales in Venezuela containing one species, *Whetzelia venequelensis*, Chardon and Toro. (See Myc. Expl. of Venezuela —Monographs of the University of Puerto Rico Ser. B. 2: 185–186. 1934. This situation requires a renaming of the smut genus. The name **Ustacystis** is therefore suggested. In a letter to the writer concerning this species some years ago, Dr. Whetzel casually suggested the appropriateness of this name. The name indicates the complex character of the species in that the germination is characteristic of a Ustilago while morphologically it is somewhat characteristic of a Urocystis. The previously published description of *Whetzelia Waldsteiniae* applies to the new names **Ustacystis Waldsteiniae** (Peck) Zundel.—GEORGE L. ZUNDEL.

THE PRODUCTION OF A PENICILLIN-LIKE FACTOR BY DERMATOPHYTES

The possible production of penicillin by organisms other than those of the *Penicillium notatum-P. chrysogenum* group is a matter of considerable scientific interest. Among the numerous surveys of various fungi for antibiotic activity is a recent report on the dermatophytes by Peck and Hewitt (Peck, Samuel M., and William L. Hewitt. The production of an antibiotic substance similar to penicillin by pathogenic fungi (dermatophytes). Public Health Reports (U. S. P. H. S.) **60**: (6) 148–153, Feb. 9, 1945).

A strain of *Trichophyton mentagrophytes*, when grown on a modified Sabouraud's broth at 30° C., was found to produce a substance antibiotic to *Staphylococcus aureus*. The antibiotic activity of the substrate appeared on the third or fourth day, increased to the ninth to fourteenth day, and then levelled off; the maximum activity obtained was equivalent to two units of sodium penicillin per cc. The addition of yeast extract, magnesium, calcium, potassium, iron, lactose, thiourea, or ascorbic acid to the culture medium did not increase the yield. The organism failed to

grow upon the corn-steep medium routinely used in commercial penicillin production with *P. notatum*, but when one per cent neopeptone was added to this substrate *T. mentagrophytes* produced an antibiotic factor in a concentration equivalent to 8–10 units per cc. of sodium penicillin. Strains of *T. violaceum*, *T. tonsurans* and *Epidermophyton floccosum* also were found to produce small amounts of an antibiotic factor, while strains of *T. rubrum*, *Microsporum canis*, and *M. audouini* did not. The antibiotic factor produced by dermatophytes was found to be similar to penicillin in respect to its enhanced production on media containing corn-steep liquor, its spectrum of activity and behavior toward penicillin-resistant organisms, its sensitivity to pH and temperature, and its destruction by clarase.—FRED WOLF.

NEW BOLATACEAE FROM FLORIDA (a preliminary communication)

While a full monographic treatment of the Boletaceae of Florida, including notes on extralimital species, is in preparation, it is felt that a preliminary account containing the new forms observed and studied there by the writer, during his tenure of a Fellowship from the Guggenheim Memorial Foundation (1942–43), would be helpful for those who are interested in the floristic or taxonomic problems involved. The total number of species observed is 53, of which 7 species and 12 varieties and subspecies are here described as new. Five new combinations are proposed.

Boletus auripes Peck var. **aureissimus** (Murr.) Sing. comb. nov. = *Ceriomyces aureissimus* Murr.

Boletus griseus Frost subsp. **Pini-caribaeae** Sing. ssp. nov. A typo sporis paulum majoribus et habitatione sub *Pinibus caribaeis* differt. Coral Gables, Fla.

Boletus Weberi Sing. sp. nov. Pileo argillaceo-avellaneo, areolato-squamuloso, sicco, 65 mm. lato; hymenophoro luteo, poris rubris ornato, circa stipitem depresso, immutabili, poris amplis; sporis 9–15.3 × 4–5.5 μ, melleis, levibus; cystidiis 14–60 × 4–6.5 μ; hyphis fibulis destitutis; sporis in cumulo olivaceo-brunneis; tramate typi *Boletorum;* stipite ad apicem rubro, basin versus olivaceo-griseolo, subfibrilloso-subpunctulato, deorsum distincte squamuloso, solido, 53 × 17 mm.; carne pallide flava, subinodora. Sub *Pinibus australibus* ad terram in Gainesville, Fla.

Boletus granulosiceps Sing. sp. nov. Pileo brunneo vel fusco, subtiliter granuloso vel velutino, 30–65 mm. lato; elementis hymenialibus in cuticula trichodermiali nullis; hymenophoro flavidulo, circa stipitem subdepresso,

poris laesis caerulescentibus, amplis; sporis 8.8–13 × 4.5–5.5 μ, levibus; cystidiis 23–56 × 6.8–11 μ, subulatis vel fusoideis; tramate typico *Boletorum;* hyphis haud fibuligeris; stipite brunneo vel sepia-granuloso vel furfuraceo, ceterum pallidiore, subaequali, 30–50 × 6–8 mm.; tomento myceliali sordide pallido vel albido; carne stipitis brunneola vel pallida, saepe caerulescente, pilei pallide flava vel pallide aurantiaca, caerulescente. In dumetis tropicalibus aestate, prope et in Miami, Fla.

Boletus subsolitarius Sing. sp. nov. Pileo cinnamomeo-fusco, ferrugineo-brunneo, atrofusco, subtiliter granuloso-furfuraceo vel subtomentoso et plerumque strato velutino tenuissimo flavo obtecto, 32–38 mm. lato; margine hymenio tecto; hymenophoro citrino vel aurato, circa stipitem subdepresso, immutabili, poris latis; sporis 8–13.5 × 4.7–5.5 μ, olivaceo-brunneis in cumulo; cystidiis fusoideis; tramate typico *Boletorum;* stipite flavido vel albidulo, apice furfuraceo, 33–38 × 11–12 mm.; mycelio tomentum luteum efformante; carne albida vel flavida, immutabili. In dumetis tropicalibus prope Miami, Fla.

Boletus rubellus Krombh. subsp. **consobrinus** Sing. ssp. nov. Pileo carmineo-subpurpureo vel olivaceo; sporis 9.2–11 × 4.7–5.4 μ; odore nauseoso vel subnullo; stipite appresse fibrilloso; mycelio laete viridi-flavo. In dumetis tropicalibus prope Miami, Fla.

Boletus rubellus Krombh. subsp. **dumetorum** Sing. ssp. nov. Pileo roseo-testaceo; stipite flocculoso-squamuloso vel subfurfuraceo; mycelio basali flavo; carne rarissime caerulescente sed superficiebus saepe tactu caerulescentibus. In dumetis tropicalibus prope Miami, Fla.

Boletus rubellus Krombh. subsp. **caribaeus** Sing. ssp. nov. Pileo testaceo, ad marginem fortiter tomentoso; sporis (9.5)–10–14.2–(16.3) × 4.2–6.5 μ; stipite flocculoso-punctulato vel subfurfuraceo, 58–67 × 10–25 mm.; mycelio sordido; carne caerulescente, inodora. Locis apricis sub *Pinibus caribaeis* prope Miami, Fla.

Boletus rubellus Krombh. subsp. **bicoloroides** Sing. ssp. nov. Pileo rubro, carmineo-rubro, partim brunnescente vel isabellascente, minute areolato-subgranuloso vel rimuloso-subtessellato, non viscido, 24–52 mm. lato; stipite carmineo-purpurascente, ad apicem flavo vel flavido, subglabro, sublevi, 28–64 × 5–12 mm.; mycelio cremeo-albida; carne caerulescente. Ad terram sub arboribus frondosis in Alachua Co., Fla.

Boletus austrinus Sing. sp. nov. Pileo brunneo-lilacino, tomentoso, 38–50 mm. lato; tubulis flavis, poris rubris vel intense aurantiacis; sporis 10.5–12.2 × 4.8–5.5 μ; tramate typico *Boletorum;* hyphis haud fibuligeris; stipite ad apicem flavo, purpureo-brunneo vel rubido-vinaceo flocculis furfuraceis causa, ad basin conspicue olivaceo-strigoso; 38–40 × 10–12 mm.; carne flava, fortiter caerulescente, miti. Sub quercubus prope Miami, Fla.

Boletus hypocarycinus Sing. sp. nov. A *B. subvelutipede* stipite albido (nec luteolo), rubro-punctulato vel rubro-lineato (nec reticulato), sublevi (nec flocculoso) et tomento strigoso basis destituto differt. Ad terram sub *Quercu virginiana* prope Gainesville, Fla.

Boletus miniatoölivaceus Frost var. **subluridus** (Murr.) Sing. comb. nov. = *Suillellus subluridus* Murr.

Boletus rubricitrinus (Murr.) Murr. var. **Fairchildianus** Sing. A typo poris rubris recedit. Fairchild Tropical Garden prope Miami, Fla.

Boletus Frostii Peck subsp. **floridanus** Sing. ssp. nov. A typo pileo roseo-purpurascente-testaceo (nec carmineo), tomentoso (nec glabro), minus viscido stipiteque normaliter reticulato (nec alveolato) differt. Sub quercubus in Gainesville atque prope Sebring, Fla.

Tylopilus minor Sing. sp. nov. A *T. felleo* statura minore, graciliore stipiteque pallidiore, saepius levi vel subtiliter tantum reticulato nec non habitatione in dumetis ("hammocks") frondosis differt. Kelley's Hammock prope Gainesville, Fla.

Tylopilus tabacinus (Peck) Sing. var. **amarus** Sing. var. nov. A typo pileo subpallidiore, glabriore et imprimis sapore amaro differt; cum typo rarius, Gainesville, Fla.

Tylopilus tabacinus (Peck) Sing. var. **dubius** Sing. var. nov. A typo pileo dilutius colorato, reticulatione apicis stipitis indistinctiore differt; cum typo rarius. Gainesville, Fla.

Tylopilus peralbidus (Snell & Beardsl.) Murr. var. **rhodoconius** Sing. var. nov. A typo sporis in cumulo roseolis differt. Gainesville, Fla.

Leccinum subglabripes (Peck) Sing. comb. nov. = *Boletus subglabripes* Peck.

Leccinum subglabripes (Peck) Sing. var. **corrugatoides** Sing. var. nov. A typo pileo dilute brunneolo-olivaceo et fortiter corrugato differt. Prope Gainesville, Fla.

Leccinum rugosiceps (Peck) Sing. comb. nov. = *Boletus rugosiceps* Peck.

Leccinum albellum (Peck) Sing. comb. nov. = *Boletus albellus* Peck.

Leccinum chalybaeum Sing. sp. nov. A *L. scabro* pileo partim chalybaeotincto et carne ardesiaco-purpurascente, dein nigrescente differt; a *L. albello* pilei superficie viscida et epithelio destituta ac saepe colore differt. Cum quercubus variis in hortis et in dumetis frondosis nec non in pinetis (cum *Quercus minima*). Prope Gainesville, Fla.—

ROLF SINGER.

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DECEMBER 31, 1943–DECEMBER 21, 1944

Balance on hand December 31, 1943:		
Cash		$ 636.80
Government bonds		940.00
Savings account		241.31
Receipts:		
Annual dues in part 1944, 1945		1860.00
Refund checks to members, not cashed		4.00
Expenditures:		
New York Botanical Garden for Mycologia	$1220.00	
Returned checks and discounts	7.18	
Postage and envelopes	51.19	
Secretarial assistance	30.25	
Mimeographing and printing	172.50	
Refunds to members	2.50	
Union American Biological Societies	15.00	
Bank service charges	2.31	
Expense of representative to Nat. Res. Council	10.16	
Expense of secretary to Cleveland meeting	32.48	
	$1543.57	
Balance on hand December 21, 1944:		
Cash	957.23	
Government bonds	940.00	
Savings account	241.31	
	$3682.11	$3682.11

(Signed) GEORGE B. CUMMINS, *Secretary-Treasurer*

Examined and found correct:

M. F. BARRUS, *Chairman of Auditing Committee*
Jan. 3, 1945.

INDEX TO VOLUME XXXVII[1]

INDEX TO AUTHORS AND TITLES

[1] This index was prepared by Jean N. Zodda.

INDEX TO GENERA AND SPECIES

New names and the final members of new combinations are in **bold face type.** Mistakes in the spelling of scientific names encountered in the text are corrected in the index.

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